THE UNIVERSITY OF ALBERTA

EVOLUTIONARY ASPECTS OF GEOGRAPHICAL VARIATION IN COLOUR AND OF PREY SELECTION IN THE BEEWOLF SPECIES *Philanthus albopilosus* CRESSON (Hymenoptera: Sphecidae)

by

© GERALD JOHN HILCHIE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

FALL, 1978

To my mother

I know that
you believe you
understand what
you think I said,
but,
I am not sure
you realize that
what you heard
is not
what I meant.

Author not known.

ABSTRACT

The phenomenon of prey selection and aspects of the life history were studied in a population of *Philanthus albopilosus* Cresson, near Empress Alberta, and compared with other populations reported in the literature. A disproportionately large number of sphecid wasps were used as prey in comparison with southern populations. Females did not appear to hunt at flowers, but appeared to hunt suitable apocritans found around the Empress dune or captured male apocritans which pursued them as potential mates. False burrows appear to have changed from primarily an anti-nest-parasite function to a visual aid in orientation to the nest. Relative absence of other species of *Philanthus* is taken to imply the specialization of wasps of *P. albopilosus* for life on sand dunes.

Differences in prey selected, nest structure and colour morphs is taken to imply geographic isolation and differentiation during Pleistocene glaciations. The Nebraska Sand Hill region is proposed as a northern refugium where differentiation of the dark northern race occurred during the Wisconsin. A southern refugium in the American Southwest is proposed for the ancestral stock of the pale southern race.

ACKNOWLEDGEMENTS

I wish to express sincere gratitude to the following persons for assistance in bringing this study to completion; my sponsor George E. Ball, who read and criticised the manuscript most constructively and members of my committee, W.G. Evans and A.L. Steiner who kindly offered advice and assistance through the course of the study.

I also wish to acknowledge John Stolz for permitting access to the study dune, John and Bert Carr for moral support and my introduction to the Empress area and Felix Sperling for assistance in drafting illustrations and checking the manuscript. Thanks are extended to Doreen Rendell for typing the thesis.

I would like to thank R.M. Bohart for the corrections and identification of the eumenid and sphecid wasps. Thanks are due to the curators of the museums from which material was borrowed.

Financial assistance is acknowledged from the following sources: The National Research Council of Canada grant A1399 held by George E. Ball and the Entomological Society of Canada Postgraduate Award.

TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

The study of the wasps of the genus *Philanthus* has recently entered into the arena of active research. Classical studies by Tinbergen (1932, 1935) using *P. triangulum* Fabricius focused on the orientation by females to concealed nests. In North America little work was done on the genus until about the 1950's. Earlier workers recorded prey of various *Philanthus* species and where the wasps lived (Rau and Rau 1918, Peckham and Peckham 1905). Reinhard (1922) concluded that females of *P. gibbosus* Cresson were better taxonomists than man. He reasoned that because of the observed specificity of the wasps to a particular group of bees (Halictidae) and the occurrence of another family (Andrenidae) represented in the prey records, that these families should be combined. It has been shown since Reinhard's early study that most members of the genus *Philanthus* are not specific to a few species or families of bees. In recent papers (Alcock 1974, Armitage 1965, Cazier and Mortenson 1965, Evans 1966b, 1970, 1975, and others) bees are reported to be the preferred prey, but in some species (*P. pulcher* Dalla Torre, *P. crabroniformis* Smith, *P. zebratus nitens* (Banks) (=*P. z. basilaris* Cresson), *P. pacificus* Cresson, and others) an expansion of prey selection has taken place: many sphecids are taken in addition to bees.

Various workers have investigated aspects of prey selection in *Philanthus*. Armitage (1965) explored aspects of prey quality, Alcock (1974) experimented with visual clues used in hunting and

Evans (1970) investigated some aspects of competition between species for prey.

Most studies on beewolves have involved ethological aspects; little information is available in relation to historical aspects which shaped the behaviours. Lorenz (1967) stated that behaviour ". . . must never be regarded as a product of change or taken as a matter of course when behaviour is found to be adapted to a corresponding point of the species environment". It is the intent of this study using behavioural and structural features to document relationships of populations against a background of Pleistocene and Holocene changes in environmental parameters.

The beewolf *P. albopilosus* was investigated during the summer of 1977 on a sand dune 11 km south of Empress, Alberta. Aspects of the behaviour were noted in relation to prey specificity and general life history. Comparisons are made with data about other populations which are recorded in the literature (Evans 1975). The Empress site along with most of Canada was glaciated during the Pleistocene. Colonization of the area occurred after the retreat of the ice and the building of the sand dunes. In order to relate the findings to other populations it is important to know the history of the population that one is studying. Different populations have been subjected to different selective pressures and these may be manifested in changes in life history and behaviour. Analysis of colour variation provides a valuable tool for the interpretation of dispersal patterns and postulations on relations between groups. This permits postulation of some of the evolutionary aspects which may have been responsible for some of the differences seen in various facets of life history and behaviour.

2. STUDY SITE

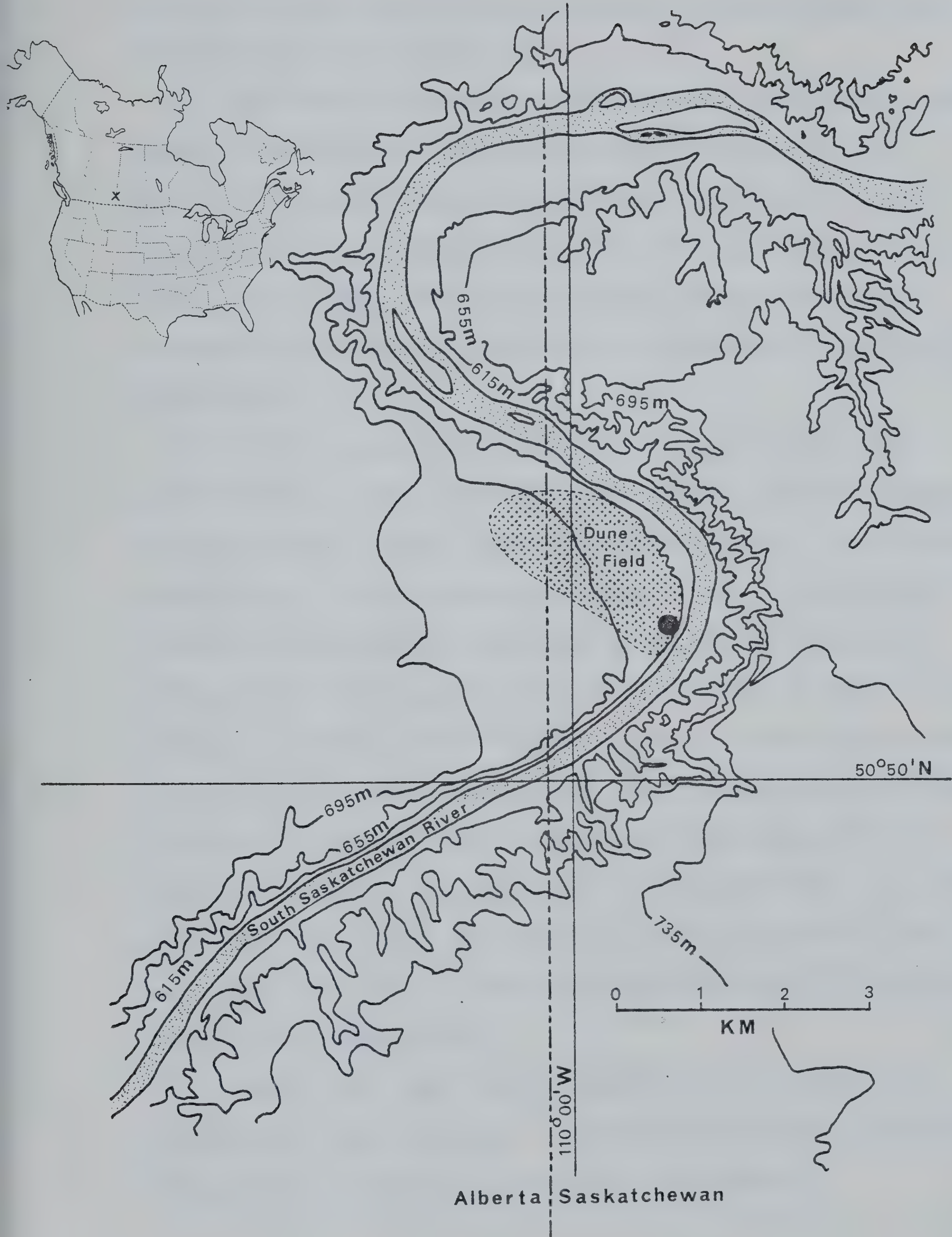
2.1 Geology and Glacial Events

The location of the study site at which research on wasps of *P. albopilosus* was conducted, was 11 km south of Empress, Alberta, east of the Alberta-Saskatchewan boundary (50° 51' 30" north, 109° 59' 27" west; Figure 1). Whitaker and Christiansen (1972) published an aerial photo of the Empress area. The dune field straddles the provincial boundary and active dunes are on both sides. Other sand dune deposits in the general area consist of the Middle Sand Hills of Alberta to the west. The Empress dunes are more or less a continuation of this system. An area of active dunes occurs about 10 km southeast of the Empress dunes, about 2 km north of Burstall, Saskatchewan. The Great Sand Hills of Saskatchewan are about 60 km to the east of the Empress dune field.

The study dune is the crest of a low bluff overlooking the South Saskatchewan River. Sand from the eastern edge of the dune blows down the bluff into the gallery forest near the river. The Empress dune field is on a layer of glacial till intermixed with lacustrine deposits. All of these overlie the Judith River formation[1] which is exposed along the river valley. The undulating terrain of the dunes, variety of substrates and close proximity to the river

[1]Bearpaw formation is present above the Judith River formation and beneath the glacial till a few km to the east or west. The Bearpaw formation was eroded away by a periglacial river at the site of the Empress dunes.

Figure 1. Map of study area, ● marks the study dune. The inset shows the relative position of the study site in North America.


655m
615m
695m
Dune
Field
50°50'N
695m
655m
South Saskatchewan River
615m
735m
0
1
2
3
KM
110°00'W
Alberta
Saskatchewan

combine to create a varied physical habitat permitting many species of insects to occupy a small area.

The fauna of the Prairie Provinces is of comparatively recent origin. The majority of organisms currently found within the provincial boundaries migrated in following the recession of the Wisconsin Ice, from refugia in the south. The major glacial advances during the Wisconsin eliminated all previous living assemblages. Summaries of the events occurring in the Wisconsin are presented in Flint (1971).

The Wisconsin Glacial Stage is postulated to have begun about 55,000 years B.P. and achieved the maximum southward expansion of the ice sheet at about 17,000 years before present. It is generally accepted that, with the southward movement of the ice, the faunal zones were either overrun (Löve 1959) in part or were displaced (Wright 1970) to the south. Extent of displacement is still a matter of much speculation. Martin (1958) argued for a wide band of tundra and taiga, Ross (1970) shows a boreal type forest abutting with the ice front but Frenzel (1973) portrays the tundra merging with the steppe on the Great Plains which splits the boreal forest into eastern and western components. Many groups of animals dependent on plant associations may have had their populations split into two main groups (Freitag 1965, Mengel 1970).

Much of the insect fauna at the study site appears to be dependent on a sandy substrate. Development and eventual colonization by the fauna is dependent on past events and conditions.

2.2 Dune Formation

At the zenith of the Wisconsin stage, a large ice sheet covered most of Canada. The massive ice sheet slowly moved southward. Soil and rocks were crushed, then ground and transported, eradicating evidence of preglacial floras and faunas.

During the time of melting of the Wisconsin ice sheet, a large mass of ice impeded drainage of water to the north. Various glacial lakes developed. Some were very large, such as glacial Lake Agassiz (Mayer-Oakes 1967). However, most were smaller transient lakes, which formed in ice-impeded river drainage basins, giving rise to extensive areas of lacustrine deposits (Edmunds 1962, Klassen 1972) comprised of clay, silt and sand deposits. Wind, reworking sandy lake bottoms and deltaic deposits, gave rise to recent dune sands (Mitchell *et al.* 1974, Allan 1937).

Requirements for development of sand dunes are; (1) a source of sand and (2) a wind to move the sand (Flint 1971). Other factors may modify the availability of sand such as geologic history of the area and climate. Geologic events control presence or absence of sand, whereas climate controls transport of sand. Xeric environments tend to develop sand dunes more readily than mesic areas. Sand dunes are found in regions where sand is available for transport (e.g. active dunes occur at Brule Lake, Alberta in the boreal forest, Dowding 1929).

The period of dune formation probably occurred in two major phases. The first began shortly after recession of the ice, before

mineral soils could be stabilized by encroaching pioneer vegetation (Ashwell 1966). This phase may have lasted for a short period.

Following initial development of dune fields a more or less mobile boreal type forest may have developed and moved north across the plains (Bryson and Wendland 1967, Wright 1970). The climate ameliorated, allowing expansion of prairie northward, beyond its present limits, reaching a maximum about 7,000 years before present. During the Hypsithermal renewed dune building would have occurred. Increased aridity reduced vegetation cover allowing increased aeolian erosion. During this warm dry period many of the xeric-tolerant and sand-adapted insects would have migrated north into new unoccupied habitats. Climatic changes have continued resulting in a reversal or general cooling since the Hypsithermal. Boreal forest has reinvaded much of the northern prairie regions and continues to slowly encroach (Löve 1959).

2.3 Present Conditions

Climate is related to the continental position of the locality, absence of modifying bodies of water, a mid-northern latitudinal location, and the rainshadow influence of the Rocky Mountains (Coupland 1950). An important feature is the low average precipitation, 22.55 cm (8.88 in.) at the town of Empress (1975 Climate of Alberta Report). Evaporation rate from free standing water in the Great Sand Hills of Saskatchewan to the east is approximately 75 cm during the frost free season (Hulett *et al.* 1966). The Empress area is the most arid region in Alberta and may be drier than any area in Saskatchewan. It is probably the aridity of the region which permits the continued

movement of the sand dunes by limiting the vegetation cover.

The Empress dunes appear to have similar plant associations to those recorded by Hulett *et al.* (1966) for the Great Sand Hills (about 60 km due east). The dunes are inhabited by several species of xeric plants (*Oryzopis hymenoides* Ricker, *Psorealea lanceolata* Pursh and *Sporobolus cryptandrus* A. Gray) which are commonly found further to the south or on sand dunes in the Great Basin (Chadwick and Dalke 1965).

3. MATERIALS AND METHODS

3.1 Materials

Study material included 39 adults of *P. albopilosus*, collected at the study site and 188 borrowed specimens. The latter are from the following institutions:

CAS California Academy of Sciences, San Franscisco.

CNC Canadian National Collection, Ottawa.

CSU Colorado State University, Fort Collins.

CUM Cornell University, Ithaca, N.Y.

MCZ Museum of Comparative Zoology, Cambridge, Mass.

SEM Snow Entomological Museum, Lawrence, Kan.

UAS University of Alberta, Strickland Museum, Edmonton.

UCB University of California, Berkeley.

UCD University of California, Davis.

USNM United States National Museum, Washington, D.C.

Also included are: 80 specimens of prey of *P. albopilosus* representing 16 apocritan taxa, whose names are listed in Table 5. An additional 200^{+} specimens listed as potential prey of *P. albopilosus* representing 45^{+} apocritan taxa, whose names are listed in Table 6, were examined.

Additionally, I examined 128 Albertan specimens of 10 species of *Philanthus*. Distribution records for these species in Alberta are included in the Appendix.

3.2 Methods

3.2.1 Investigation of Geographical Variation

Examination of the trends was accomplished through the use of a Compound Character Index (Sneath and Sokal 1973). This approach was used because of lack of a single consistent diagnostic character or group of characters. The results are summarized in Figures 5 and 6. The characters used to compile the index values seem to be the only ones available. Character states used are noted in the following subsections accompanied with notes.

Females. Eleven characters whose states were constant in a given locality varied geographically. Many additional characters, such as pubescence length and density, were examined but they varied inconsistently. Variation in density of pile may result from age of the wasp and variable abrasion by sand.

1. Frons: An estimate of percentage of the area marked with yellow was made. The area considered was delimited at the apex of the head by a line of the ocular grid (microscope) placed in contact with the base of the median ocelli, which extended, contracting both compound eyes. Estimates of the coloured area were made to the nearest 5%. Maximum ranking was given a value of 99%, the border between the clypeus and frons was dark and assumed to be 1%.

2. Clypeus: The clypeus was scored in a similar manner with a maximum score of 99%. The area was delimited by the dorsal suture with the frons and the ventral suture with the labrum.

3. Vertex of Head: The pattern of maculations were given index values ranging from 0 for no maculations to 9 for a solid bar.

4. Scutellum: The character states ranged from entirely black through two spots to a single large median spot with index values of 0 to 9 respectively.

5. Mesonotum: Three character states were recognized; black, two lateral spots and a single tranverse band with index values of 0, 5 and 9 respectively.

6. Pronotal Collar: Five character state classes were recognized: black, small lateral spots, large oblong lateral spots, broken band and a continuous transverse band which were assigned index values of 0, 2, 5, 7 and 9 respectively.

7. Scutum: An estimate of percentage colour was taken Range was from 0% to 50%. Estimates were made to the nearest 5%. Some error may be present, but the trends are still apparent.

8. Propodeum: An estimate of percentage colour was taken, which ranged from 0% to 80%. Maculations on the dorsal and lateral aspects were used in the estimate. The posterior exposure of the propodeum was excluded from the estimate because it was often obscured by the abdomen in many specimens.

9. First Abdominal Tergite: An estimate of the area of light color was made from the dorsal aspect. Values varied from 0% to 95%, estimates were made to the nearest 5%.

10. Abdominal Tergite Two: Color was estimated as for the first abdominal tergite with values ranging from 20% to 99%.

11. Abdominal Sternal Spots: These are located on the lateral portion of the sternal sclerites, one spot per sclerite per side.

The total number of spots on the right side were recorded and assigned an index value.

Table 1 summarizes character states examined and the assigned index values for each state. Low values were assigned to black or minimum color and high values to the maximum amount of yellow. All character states were given equal weighting. Figures 7 and 8 show some of the variation in maculation for southern and northern female wasps.

Males. The males showed considerably less variation than did the females. Five characters vary but not markedly so. Thus values for continual characters had a range of score of five (0-4), in contrast with females with a range of score of ten (0-9).

1. Pronotal Collar: Maculations varied from solid black to a continuous bar of yellow.

2. Scutellum: Only two character states were recognized; presence or absence of two yellow spots.

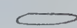
3. Colour of Abdomen: Most frequent colour for males is bright lemon yellow, tinted in some with orange, in others the colour is a rich orange to red. The red or darker colour is assigned an index value of 0 and yellow the index value of 4.

4. Pronotal Lobe: Presence or absence of colour was noted and given a value of 0 (no colour) or 4 (colour).

5. Fourth Abdominal Tergite: Maculation varied from a single median spot (index value 0), a series of spots, median and lateral (index value 2) and a band spanning the width of the tergite (index value 4).

Table 1

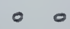
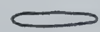
Compound character index values assigned to selected character states in female wasps of *Philanthus albopilosus*.

Character \ Index value	0	1	2	3	4	5	6	7	8	9
1. frons	*0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99
2. clypeus	*0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99
3. vertex of head	black	-		-			-		-	
4. scutellum	black	-		-			-		-	
5. mesonotum	black	-		-	-		-	-	-	
6. pronotal collar	black	-		-	-		-		-	
7. scutum	*0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49
8. proprodeum	*0-7	8-15	16-23	24-31	32-39	40-47	48-55	56-63	64-71	72-79
9. abdominal tergite 1	*0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99
10. abdominal tergite 2	*20-27	28-35	36-43	44-51	52-59	60-67	68-75	76-83	84-91	92-99
11. abdominal sternal spots	0	-	1	-	-	2	-	3	-	4

*Denotes percentage area of light colored maculations. Diagrams denote relative size and shape of maculation, anterior is towards top of column.

Table 2

Compound character index values assigned to selected character states in male wasps of *Philanthus albopilosus* Cresson.

Character \ Index Value	0	1	2	3	4
1. pronotal collar	black				
2. scutellum	black	-	-	-	
3. abdominal colour	orange	-	orangish yellow	-	yellow
4. pronotal lobe	black	-	-	-	
5. abdominal band on tergite 4		-		-	

Diagrams denote relative shape and size of maculation.

Table 2 summarizes the characters used and the weight applied to each. Figure 9 illustrates the head and abdomen of a male.

A score of 0 typified the extreme dark male and a score of 20 the extreme light male. Few specimens fell in either of these categories. Variation appears clinal with darkest males in the north and the lightest in the south.

In addition to the five characters used in the compound character index, the genitalia were extracted and examined. No useful differences were found. This is consistent with observations by Bohart and Grissell (1975) and Strandtmann (1946) who report that variability in male genitalia in *Philanthus* between distinct species is of little or no taxonomic importance.

3.2.2 Investigation of Life History

During the summer of 1977 the wasp species *P. albopilosus* was studied on a sand dune 11 km south of Empress. Data from previous years were incorporated with the data from the 1977 season.

Early in the field season nests of *P. albopilosus* were left undisturbed to facilitate observations of behaviour. Each nest was staked with a stick about 20 cm in length at a distance of 15 to 20 cm south of the nest entrance. Vestibules of most of the nests sloped eastward into the dune.

Each nest was assigned a number. Most nests were located by watching a potential nesting area for prey-laden female wasps. Potential nesting areas often had males patrolling and landing on the sand. When false burrows were present the nests were staked and watched.

In conjunction with marking nests, individual wasps were marked with small dabs of Testors brand model paint on the scutum. Five colours were used in two positions (right and left side). Lack of a dab of paint was taken to be a sixth colour in conjunction with any of the other colours. In a three-position system using black as the sixth colour there are $6^3 - 1$ or 215 combinations. Additional combinations could be made by adding more colours or positions. Females were marked by restraining them in a fold of a light collecting net, such that the dorsal surface of the thorax was exposed. After marking, each female was temporarily detained to permit the paint to dry. It was found through experience that if a female was captured immediately after exiting and before the orientaion flight, she did not return to the nest. If the female was caught before entry (often with prey) or after orientation the probability of sighting the wasp again was high. When caught before entry and marked, the wasp returned, opened the nest, entered, then exited, closed the nest, oriented then departed. Many marked females continued provisioning of their nests. Notes were taken on rates of provisioning and duration of the nests.

Males of *P. albopilosus* were not studied at the Empress site. From casual observations the males appeared to behave like those described by Evans (1975).

3.2.3 Investigation of Prey Selection

Nests were initially observed while attempting to record the prey being brought back by the females. Toward the end of July in an effort to determine more accurately the prey species many staked

nests were sacrificed in the evening when the female was inside with a day's capture of prey at the end of the vestibule. Prey and the beewolf were collected and placed in 75% alcohol solution. Voucher specimens are in the Strickland Museum (University of Alberta). A list of prey collected from nests and individual wasps is presented in Table 5.

Observing where the beewolf hunted was tried, by following outward-bound females. However females travelled too fast to be tracked and were lost when they entered the vegetation around the dune.

In conjunction with examination of what was caught by the female beewolf, a sample of what may be available as potential prey was made. Potential prey was sampled by sweeping vegetation around the dune in areas thought to be potential hunting areas. Collection of bees and wasps from flowers was made when blossoms of *Psoralea* and *Solidago* were present. Dune-inhabiting bees and wasps were sampled by netting these insects as they were encountered. Common species were initially sampled after which they were passed by. Notes on relative abundance were made for some of the common species. Also included in the survey are Apocrita which were caught at the study site prior to 1977. Results are summarized in Table 6.

4. LIFE HISTORY IN GENERAL

Populations of *P. albopilosus* are readily overlooked because of very localized distribution and this may be the reason for the paucity of studies. Evans and Lin (1959) published a note on an aspect of way of life based on excavation of a single nest. Evans (1975) compared two widely separated populations, one from Albany, New York and the other from Roggen, Colorado.

Choice of habitat tends to bias collecting of specimens of *P. albopilosus*. They are easily overlooked by collectors seeking wasps in more productive areas around sand dunes. Distribution of dune and blowout habitats probably restricts distribution of *P. albopilosus* on a local level. Few other wasps nest in the same region of the dune. At present it is not known how restricted the wasps are in choosing nesting sites. From information gathered (data tags, field experience) I believe that the wasps of *P. albopilosus* are very closely associated with a dune type of environment.

4.1 Empress Dunes Population of *P. albopilosus*

Females of *P. albopilosus* typically nest on margins of broad flat bare areas of the sand dune. Nests are in a zone of lightly drifting sand, away from vegetation.

A nest is of elaborate design. The entrance of a new nest is concealed by a sand closure and a number of false burrows may be

present, ranging from zero to six. Proportion of nests at the Empress site lacking false burrows is not known. Numbers of false burrows were not recorded. They are constructed immediately following completion of a nest at the time of initial closure, but are not maintained, and some fill with loose sand in a few hours. From the nest entrance a horizontal or nearly horizontal vestibule extends for about 25 cm, although accurate measurements were not taken. The vestibule terminates at the beginning of a vertical gallery. Depth is unknown as provisioned cells were not found. Figure 2b shows the profile of a burrow from New York which is similar to the burrows found at Empress.

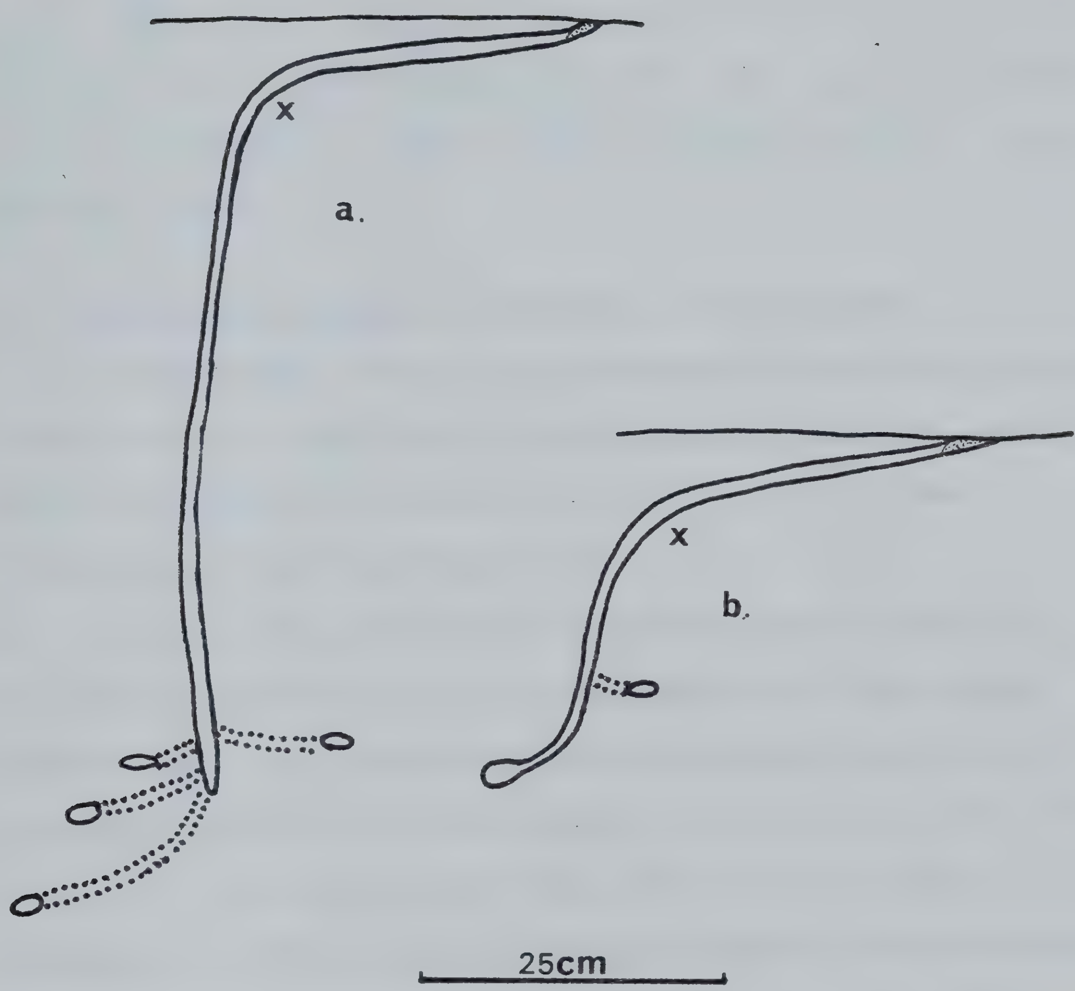
Prey is stored at the end of the vestibule until a cell is prepared. Prey consisted of bees and wasps and their significance will be discussed in a later section.

Females occupy their nest for a relatively short time, usually one or two days. Nests were provisioned from late June through July into early August.

Life span for adults of *P. albopilosus* is as yet undocumented. I assume that females live and provision their nests over a period of about three weeks. This figure was arrived at from life spans of other species of *Philanthus*, *P. gibbosus* (Reinhard 1922) and *P. crabroniformis* (Alcock 1974).

Sightings of marked wasps of *P. albopilosus* at the study site were rare. The only record was of a wasp provisioning a new nest, 11 days after marking. Life span of adults may be longer or shorter than three weeks depending on local conditions.

Figure 2. Profiles of active nests of *Philanthus albopilosus*. Figure 2a from near Roggen, Colorado. Figure 2b from near Albany, New York. "X" indicates position where prey is stored. Nest profiles are after Evans (1975).


x
a.
x
b.
25cm

Duration of the larval stage is unknown. In populations which are multivoltine it may be inferred to be of short duration, possibly a few days to weeks. Populations which are univoltine may have a diapause in either larval or pupal stages. An estimate of larval life span cannot be made.

Males in the Empress area typically perched on the sand in alert positions. They frequently flew off following passing insects and on a few occasions grappled with prey-burdened females. Matings were not observed.

4.2 Comparisons with Other Populations of *P. albopilosus*

Evans (1975) studied nesting behaviour of two widely separated populations of *P. albopilosus*. For the Empress population, my data about nest construction and location, nest duration and male behaviour agree well with Evans' data.

Evans (1975) reported that in borrows built by females of the Colorado population, cells at the terminal end of the gallery averaged about 2.5 times deeper than those in the Albany, New York population. Range of variation does not overlap, Figure 2 (New York, 13-25 cm $\bar{X}$ = 19.2 cm; Colorado 31-62 cm $\bar{X}$ = 52.0 cm). Depth of galleries at the Empress site are unknown in spite of many excavation attempts. The gallery was lost at a shallow depth (15 to 20 cm).

If depth of the burrow reflects past evolutionary interactions and not a response to local conditions, presence of shallow burrows in the northern populations may reflect past climatic stresses for the wasps. Winter temperatures may not be very important but time and rate of ground thaw may be. Cells closer to the surface experience warming earlier in the season. This permits a longer period of

development, which would allow colonization of areas with a shorter growing season. The opposite may be true in southern areas: intense heating of the sand by the sun may be lethal to cells near the surface (Chapman *et al* 1926) which would select for deep nests.

Data of adult activity periods were obtained from locality labels; dates were consolidated into four day units and graphically illustrated in Figure 3 using the area groups illustrated in Figure 4. Northern populations (Areas 7, 8, 9, 10, 11 and 12) appeared to have one main generation active during July, and in some (Areas 7, 8 and 9) there appears to be a smaller second generation in early September. In the southern population groups, collection dates range from May 27 to as late as October 17 indicated the possibility of continuous generations (multivoltine).

In all areas except Empress (Area 12), data presented represent collecting dates, not activity of the adults. On Histogram 12, Figure 3, the dashed line represents the dates when collecting was attempted. Here negative evidence is an indicator of when the beewolves were not present.

Females at the Empress study site appear to occupy nests for a shorter period of time than either the Colorado or New York populations (Evans 1975). This may reflect fewer cells per nest. Evans reports that of 26 marked nests in Colorado only a few were active after a few days. In the New York sample of marked nests (n=5), two were active three days later (Table 3). A maximum of four cells per nest has been reported by Evans.

Figure 3. Temporal distribution of adult *Philanthus albopilosus*. Areas are those illustrated in Figure 4. Dashed line above histogram for Area 12 (Empress) indicates collecting dates at the study site.

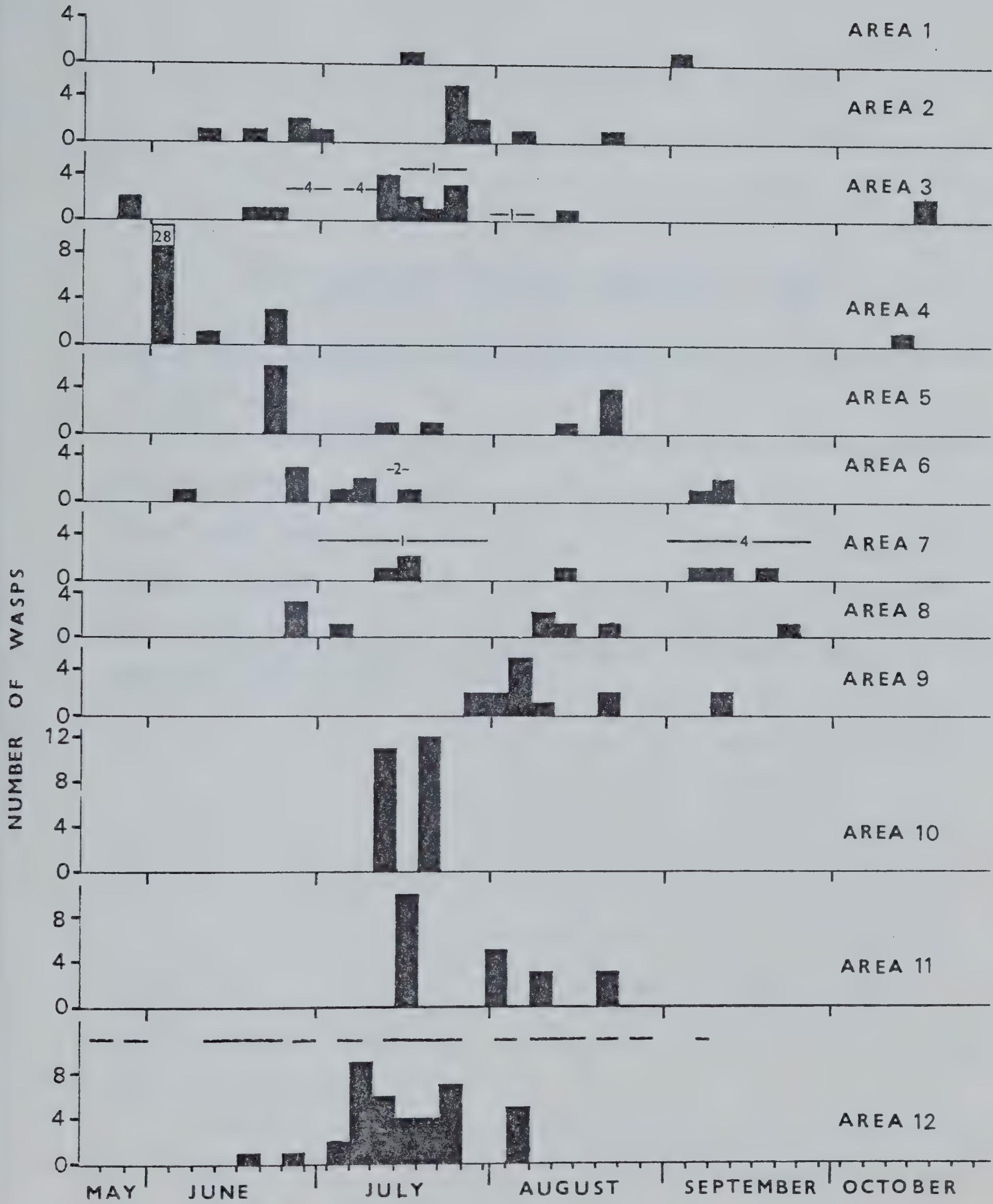

AREA 1
AREA 2
AREA 3
AREA 4
AREA 5
AREA 6
AREA 7
AREA 8
AREA 9
AREA 10
AREA 11
AREA 12
28
NUMBER OF WASPS
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER

Table 3

Duration of nest occupancy on the Empress dunes in comparison with Evans' (1975) study sites.

Locality \ Day	0	1	2	3	4
Empress, Alberta	15	2	0	-	-
Albany, New York	5	-	-	2	-
Roggen, Colorado	26	-	-	-	few

Numbers refer to the nests observed. Day zero refers to when the nests were first observed.

4.3 Distinctive Features of the Empress Dunes Population

The Empress population does not have many distinctive features differentiating it from the New York population, other than possibly fewer cells per nest. In comparison with the Colorado population the depth of the nest may be different with the Colorado populations digging deeper galleries. Differences in prey selection and colour variation are present but will be discussed in a later section.

4.4 Other Species of *Philanthus* in the Study Area

The species *P. albopilosus* was the dominant *Philanthus* on the Empress dunes. Two specimens of *P. psyche* Dunning were captured, one amongst the vegetation and the other over bare sand. Nests were not found. Evans (1975) reports that *P. psyche* occurs in the same type of habitat as *P. albopilosus*. When the two species of beewolves occur together, *P. psyche* females nest amongst the vegetation along the edge of the dune and *P. albopilosus* females nest on bare sand.

A single specimen of *P. solivagus* Say was caught along the river. For a brief account of way of life see Evans and Lin (1959). *Philanthus solivagus* is reported to be a common species in north-eastern U.S.A. Females prey on bees (mostly halictids) and some wasps (sphecids and vespids).

Six specimens of *P. ventilabris* Fabricius were captured, some of which were in association with *Solidago* flowers. Evans and Lin (1959) reported nesting records in flat sandy soil and Krombein (1936) records this species from a sand pit.

One specimen of *P. gibbosus* (Fabricius) was captured at the study site. Wasps of this species nest in sandy soil. Cazier and Mortenson (1965) induced females to nest in areas where the ground was previously soaked with water. The fine porous sand of the Empress dune holds little moisture near the surface. Nesting sites of *P. gibbosus* in the Empress area are probably located along the river in damper soil. This may explain why females were seldom seen.

The sixth species of *Philanthus* found at the Empress study site was *P. gloriosus* Cresson, on which little information is available on its way of life. Specimens of *P. gloriosus* were the largest beewolves at the study site.

5. FALSE BURROWS

A false burrow or accessory burrow is defined by Evans (1964b) as "any burrow started from the soil surface in close proximity to the true burrow and made by the same individual". Females of *P. albopilosus* construct accessory burrow after completion of the nest, and there may be as many as six. The classic interpretation by Evans (1964b) is that these burrows serve to dupe the nest parasites into ovipositing in an inappropriate place or to divert the parasite into exploring empty holes where there are no hosts.

The habit of preparing false burrows appears to have evolved several times in the Sphecidae, in association with nesting in open sandy environments. Table 4 summarizes the occurrence of false burrows in various taxa of sphecids with information on type of false burrow, number of false burrows, duration, maintenance, first occurrence in time, and pertinent notes on life history.

Wasps which maintain or repair false burrows dig them early in the history of the nest, usually during or after the initial closure. The habit is thought to have evolved from quarrying soil for a closure of the nest. Maintaining the false burrows would simply entail the use of one or a few of the holes as a source of soil for later closures. Maintenance of false burrows would provide continued protection from some nest parasites.

Associated with species which dig false burrows early but do not maintain them, are various behavioural features which may reduce

the effect of nest parasitism. Females of *Bembix* progressively provision their nests. If parasites do enter the nest the female may be able to supply enough prey, permitting survival of both the larvae and parasite, thus reducing impact of parasitism. This reduction removes some of the selective advantage of maintaining the false burrows.

Females of one species, *B. texana* Cresson, construct false burrows during final closure. Debris is removed from the nest and parasites may be swept out during this process -- but it is not known if this happens. Nonetheless, false burrows prepared at this time may offer protection from invasion by parasites, at least until environmental effects obliterate all traces of the burrow.

Construction and failure to maintain the false burrows in a mass-provisioning species (*P. albopilosus*) is unexpected. The pattern would be expected in species whose females practice progressive provisioning. The association of provisioning and nesting behaviours has changed, which may indicate a difference in function.

The hypothesis which I propose is the change of function of the false burrows made by *P. albopilosus* from that of an anti-nest-parasite device to that of a visual marker aiding in initial orientation to the nest in a habitat with an unstable substrate. A large premium would be placed on learning the correct location of the nest without advertising its true entrance during the first orientation flight. This would permit the female to take bearings on distant land marks and visually relate the location of her nest (van Iersel 1964). After orientation, the false burrows would no longer have a function, would not be maintained and would

Table 4

Occurrence of accessory burrows in the Sphecidae.

Taxon	Number of false burrows	Type of false burrow	Duration of false burrow	Type of provision-ing	Care of false burrows	First occurrence of false burrow	Notes	Investigator
Philanthus albopilosus Cresson	0-6	lt	sh	ma	nm	er	--	Evans 1975
P. lepidus Cresson	1-5	lt	lo	ma	mt	er	--	Evans 1964a
P. cornatus Fabricius	1	--	--	ma	--	--	--	Tsuneki 1943
Sphex argentatus Mocsary	2-3	lt	lo	--	mt	er	--	Tsuneki 1963
Stizus pulcherrimus Smith	2-4	lt	lo	--	mt	er	--	Tsuneki 1943
Bembix sayi Cresson	1	bh	sh	pr	nm	la	--	Evans 1964b, 1966a
B. texana Cresson	0-2	lt	sh	pr	nm	er	cc	Evans 1964b, 1966a
B. troglodytes Handlirsch	0-1	lt	sh	pr	--	--	--	Evans 1964b, 1966a
B. pruinosa Fox	1	lt	--	--	--	--	--	Evans 1964b, 1966a
B. amoena Handlirsch	0-1	fu	--	pr	--	at	fc	Evans 1964b, 1966a
B. niponica Smith	?	ho	--	pr	--	--	fc	Tsuneki 1956

Symbols used: at, any time; bh, back hole; cc, cell cleaning; er, early; fc, fill for closure; fu, furrow; ho, hole; la, late; lo, long; lt, lateral; ma, mass; mt, maintained; nt, not maintained; pr, progressive; sh, short.

fill with drifting sand.

A similar land mark function has been attributed to the mound building activities of *Bembix littoralis* Turner. Evans and Matthews (1975) reported *B. littoralis* females building a mound of soil at the entrance of their burrow, which may serve as a species specific marker identifying the nest location when other species of sand wasps were present.

6. PREY SELECTION

Insects are not very intelligent. Their neural circuitry does not permit accumulation of large quantities of stored information. This does not imply insects can not learn: on the contrary, many site-affixed insects are programmed for learning important aspects of the environment. Tinbergen (1935) experimented with orientation abilities of *Philanthus triangulum* to a concealed nest. Von Frisch (1953) experimented with honey bees (*Apis mellifera* L.), releasing workers of different ages at various distances from the parental hive. Bees which had learned the landscape returned, the older the bee the greater the distance. Orientation toward a particular site is governed by experience which is recorded in genetically controlled learning. The task of orientation has one ultimate goal related to survival: to get the females back to their nest with provisions for their larvae. There is little room for plasticity in orientation outcome; either the animal succeeds in returning or does not and so fails to provision the nest.

Prey specificity is largely dependent on a genetic basis. Various evolutionary and environmental factors interact, being expressed as a mosaic of different wasp populations using different complexes of prey species (Evans 1966c). Precise entrainment to a particular group may be detrimental as prey species are subject to fluctuations in relative abundance. A plastic response to a complex of groups of prey is a better evolutionary strategy.

Females of most philanthine genera use various apoids and to a lesser degree, other wasps. Females of most species of *Philanthus* show a preference for halictid bees, with a marked tendency of some species to use sphecids as prey (Armitage 1965, Evans 1970). Females of *Aphilanthops* prey exclusively on ants of the genus *Formica* (Bohart and Grissell 1975). Remarkably, females of most species of *Cerceris* and those of all species of *Eucerceris* prey on Coleoptera (Bohart and Menke 1976). This is exceptional among the Philanthinae, but illustrates very well the sorts of differences that can occur among groups sufficiently closely related to be included in a single subfamily. These last two genera are closely related to one another, but are quite distantly related to *Philanthus* (Bohart and Menke 1976).

In this section, results of observations are presented about prey selected by females of *P. albopilosus*. From these observations inferences are made about methods of prey capture and factors that determine acceptability of prey. These inferences are discussed as the basis for consideration of a more general hypothesis about selection of prey by females of *P. albopilosus*: 1) on the Empress dune, and 2), elsewhere in the range of the species.

6.1 The Empress Dunes Population of *P. albopilosus*

Females of *P. albopilosus* captured a varied group of prey including members of three families of wasps and three families of bees. Prey records are listed in Table 5. The wasps used as prey were members of nine species with a total of 30 individuals: 26 males and four females. *Aphilanthops frigidus* (F. Smith) males were

Table 5

Prey records for wasps of *Philanthus albopilosus*
Empress study site.

	♀	♂
Ichneumonidae		
genus species	1	0
Eumenidae		
Stenodynerus anormis (Say)	0	1
Sphecidae		
Aphilanthops frigidus (F. Smith)	0	17
Crabro denningi R. Bohart	0	1
Diodontus sp.	1	3
Mellinus abdominalis Cresson	0	1
Microbembex monodonta (Say)	1	1
Podalonia violaceipennis (Lep.)	0	1
Tachysphex tarsatus (Say)	1	0
Tachysphex exsectus W. Fox	0	1
10 species of wasps; 30 prey records		
Halictidae		
Agapostemon sp.	0	1
Halictus rubicundus Christ	0	23
Halictus sp.	1	0
Lasioglossum sp.	0	2
Sphecodes sp.	0	3
Colletidae		
Colletes sp.	0	19
Megachilidae		
Osmia sp.	1	0
7 species of bees; 50 prey records		
total prey records for each sex	6	74

the most common wasps used as prey (17 individuals).

The 48 male and two female bees captured as prey were members of seven species. Most of the prey records were divided between males of two species, *Halictus rubicundus* (n=23) and *Colletes* sp. (n=19).

Prey records total 80, of which 37.5% are wasps and 92.5% are male apocritans.

Prey ranged in length from 5 to 11 mm with a few wasps measuring 14 mm and 19.5 mm. The most commonly used prey ranged from 8 to 11 mm.

In conjunction with this study, I collected wasps generally in the study area, to establish a basis for comparing what was taken with what was available. Table 6 contains data on apocritans whose adults seem to be within the size range preferred by females of *P. albopilosus*. See the Discussion section.

Rates of provisioning are relatively slow. One wasp (#004) returned in five minutes with prey; another wasp completed the task in 55 minutes. Provisioning rates for a few wasps are shown in Table 7.

I also considered provisioning rates as a function of total daily catch. These may be tallied by excavation of the nest after provisioning activities have ceased, usually by 1800 h standard time. Contents of the nest are stored at the end of the vestibule until a cell is constructed. I do not know when this takes place but the activity appears to occur at a later time, possibly the next day. Table 8 summarizes the number of prey per vestibule. It appears that the females capture about five prey for each cell provisioned.

Table 6

Some taxa of Hymenoptera collected in the Empress area which are available as potential prey* to the beewolf *Philanthus albopilosus*.

Taxa	Abundance	Association	Specimens collected ♀	Specimens collected ♂
Sphecidae				
Ammophila spp.	a	nest on dune	35	14
# *Aphilanthops frigidus* (Smith)	c	on dune, scurf pea	2	4
Astata sp.	nc	on dune	-	2
Cerceris echo Mickel	nc		2	-
# *Crabro denningi* R. Bohart	a	on dune	?	9
Crabro spp.	a	on dune, scurf pea	12	-
crabronids, other	nc		1	-
# *Diodontus* sp.	nc	on dune	-	2
Gorytes sp.	nc		1	1
# *Mellinus abdominalis* Cresson	a	Sweeping, on dune	-	7
# *Microbembex monodonta* (Say)	a	on dune in colonies	20+	10+
Oxybelus sp.	nc	on dune	1	2
# *Podalonia violaceipennis* (Lep.)	c	nest on dune	1	5
Podalonia spp.	a	nest on dune	10+	20+
Psenulus sp.	nc	on dune	-	1
# *Tachysphex tarsatus* (Say)	a	on dune	9	12
# *Tachysphex* spp.	a	on dune	3	5
Tachytes sp.	nc		-	1
Eumenidae				
Cephalodynerus sp. 1	c	on dune, scurf pea	1	5
Cephalodynerus sp. 2	nc	on dune	-	1
# *Stenodynerus* sp.	nc		-	1
Halictidae				
# *Agapostemon* sp.	a	on dune, sweeping, scurf pea	6	4
# *Halictus rubicundus* Christ.	nc	on dune	1	-
# *Halictus* spp.	nc	on dune, on plants	2	1

Table 6 (continued)

Taxa	Abundance	Association	Specimens collected ♀	♂
Sphecidae				
# *Lasioglossum* sp.	nc	sweeping	-	1
# *Sphecodes* sp. 1	a	on dune, goldenrod	4	2
Sphecodes sp. 2	nc	on dune	1	-
Colletidae				
# *Colletes* sp.	a	sweeping	-	1
Andrenidae				
Perdita sp.	nc	sweeping	-	1
Anthophoridae				
Nomada vicina Cresson	a	on dune	5	-
Megachilidae				
Anthidium sp.	a	on scurf pea	5	-
Megachile sp.	c	sweeping, scurf pea	3	-
# *Osmia* sp.	nc	on dune	2	-
Mutillidae				
Dasymutilla bioculata (Cresson)	a	on dune	20+	10+
Ichneumonidae				
many species	-	in vegetated areas	5	2

*This list is a sample of potential prey defined as Apocrita Hymenoptera from 5 to 11 mm if heavy bodied or a maximum of 20 mm if slender bodied and active during the months of June, July and August. This list is a guide and many species and general have been overlooked because of sampling procedures. I assume that those species missed do not comprise a large portion of the potential spectrum of prey species.

Symbols used: a, abundant; c, common; nc, not common; # taxa used as prey but excluding prey records.

Table 7

Provisioning rates for selected females of
Philanthus albopilosus.

Individual	Leaving Time h	Returning Time h	Time Elapsed
004	1325	1330	5 min.
006	1336	1342	6 min.
007	before 0858	1030	92 min.
	1036	1050	14 min.
014	1250	1345	55 min.
019	1158	1220	22 min.

Time intervals are from when the female left the nest to when she returned with prey.

Table 8

Number of prey per nest.

Date	Number of nests	Prey record number	Number of prey
20:VII:76	1	4-7	4
16:VII:77	2	11-16, 18-22	11
25:VII:77	5	30-53	24
5:VIII:77	5	54-80	27
	13 nests		66 prey records

Calculations are based on nests dug up after 1800 h when no further hunting was expected. The average number of prey per nest is 5.1 individuals.

Nests were occupied for a maximum of two days (digging to abandonment) with most being occupied for a single day (about 24 hours).

Because of the very slow provisioning rate, my efforts to trace hunting sites were thwarted. On August 4 I observed a female *P. albopilosus* attack and capture prey. A beewolf cruising about 50 to 60 cm above the sand near a colony of *Microbembex monodonta* (Say) wasps, dived to the ground, and attacked and captured one of the *Microbembex*. The latter individual was either flying near or resting on the sand. I did not see it until the beewolf made contact. Beewolf and prey were collected immediately. The *Microbembex* is Prey Record No. 54. Females of *Microbembex monodonta* nested along the edges of the sand dune.

Throughout the entire 1977 field season, wasps of *P. albopilosus* were not observed at flowers, but this does not mean that they do not visit flowers. If female *P. albopilosus* did hunt at flowers I would expect that the number of female bees taken as prey would increase or exceed the number of males captured. Females of several species of bees of the correct approximate size to be used as prey were quite common on flowers on or near the dune.

6.2 Comparisons with Other Populations of *P. albopilosus*

Evans (1975) reported a prey capture pattern similar to the Empress population of *P. albopilosus* from Albany, New York. Females in the Albany population captured wasps of two families (Sphecidae and Eumenidae) and captured bees of three families (Colletidae, Halictidae and Andrenidae). Prey records of wasps comprised 17.3% of the total catch, and of male Apocrita, 79.1%.

Exact duplication of the results is unlikely as beewolf populations are widely separated geographically and may have a different mixture of potential prey species available.

On reviewing prey data presented for the Colorado population of *P. albopilosus*, a marked discrepancy is evident. Number of species and families of Hymenoptera decline, for 73 prey records include only four species of two families of bees (Halictidae and Colletidae). Because few populations were examined, difference may be due in part to sampling error.

Evans and Lin (1959) noted the contents of a single nest of *P. albopilosus* in Tuba City, Arizona. The nest contained one halictid and four anthophorid bees. The sample is too small to indicate possible trends.

Many authors (Armitage 1965, Evans 1966b, 1970, Reinhard 1922, Tinbergen 1935, and others) have reported female *Philanthus* hunting at flowers. Pinned specimens of *P. albopilosus* from several localities bear flower capture data. These are as follows: Colorado, on *Tamarix*; Arizona, on *Poliomintha* and on *Parvella*. There are no flower capture data for any northern localities.

6.3 Discussion

The data presented show that prey selected by females of *P. albopilosus* is typical for philanthines generally, *i.e.*, principally aculeate hymenopterans are taken. The data also show that a mixture of bees and wasps is taken, and this is consistent with Evans' (1975) observations on a colony of *P. albopilosus* in New York. However, information of this sort is only the first step

to understanding the general phenomenon of prey selection for this species. A general hypothesis is required to guide further inquiry. The hypothesis will serve as the point of departure for establishing predictions, and in turn these form the basis for assembly of additional data.

An organism specializing on a particular group of prey species has many factors influencing choice. Physical constraints of the predatory apparatus and behavioural restraints control which type of prey are suitable. Behavioural restraints may involve regulation of where the organism hunts, type of prey and quality of prey acceptable. Availability of suitable prey and its relative abundance will affect what is caught by the predator.

Prey selected by female *P. albopilosus* on the Empress dunes consists of mostly bees and sphecid wasps. Members of three families of bees were used (n=50) with *Halictus rubicundus* (n=23) and *Colletes* sp. (n=19) being the primary prey species. Members of three families of wasps were used (n=30), of which most were sphecids (n=28). The primary sphecid species whose members were used as prey was *Aphilanthops frigidus* (n=17).

In another study, Armitage (1965) investigated prey selection by females of the beewolf *P. bicinctus* (Mickel). The data from his experiments demonstrated that females rejected old bumble bees in preference to capturing younger bees. Recognition of suitable prey was made after contact with a bee.

Alcock (1974) demonstrated that females of *P. crabroniformis* Smith attacked balsawood models about the size of potential prey. Attack was greatly influenced by colour: dark models were attacked

at a high frequency in comparison with light coloured models. Beewolf females did not capture (defined as grapple and sting the model) any model but did capture suitable prey when presented under the same conditions. Alcock observed in the field that females struck bumblebees, ants and halictid-sized flower buds. Female *P. crabroniformis* appear to hunt visually, attacking suitable sized and coloured objects. Grappling and stinging occurred only when members of prey species were encountered. Tinbergen (1935) reported that olfaction was important in prey discrimination for females of *P. triangulum*. Aspects such as those mentioned above make it difficult to predict what should be captured in relation to what is potentially available. It appears that prey specificity for a given species may be adequately predicted only by examining past performance.

Certain parameters are measurable and are of some use in predicting exploitation of a particular species of bee or wasp rather than another species. Evans (1970) used length of prey, but this is a rather imprecise indicator of potential prey species because body form of bees and wasps varies considerably in relation to length. Measure of mass would be superior; however, live weights are required and these are difficult to obtain under field conditions. Mass or weight would place an upper limit on size of prey used, because a beewolf must carry prey to the nest by means of flight. Lower size limits may be related to ability to grasp and manipulate the victim. However optimum prey size may also be influenced by competitive exclusion (Evans 1970). Nevertheless, I use body length to estimate prey acceptability.

Potential prey are regarded as adult apocritans whose minimum body length is 5 mm and maximum length is 11 mm for stout forms and 20 mm for slender forms. These figures place some restraint on which species of bees and wasps may serve as prey.

Table 6 lists names of apocritans inhabiting the study area whose adults are of a suitable size to serve as prey for females of *P. albopilosus*. As an indicator of where females of *P. albopilosus* may be hunting, notes are included on locations and relative abundance of potential prey.

In comparing what female beewolves caught and what was available, Tables 5 and 6 show little similarity.[2] Females seem to specialize on a few common species near but not right on the dune. If female beewolves hunted primarily on the dune it is expected that a number of genera representative of dune dwellers would have been better represented as prey. Another discrepancy is evident; in Table 5 there is a heavy bias toward males of the dominant species of prey. Males of many species of bees and wasps frequent flowers or positions near flowers while seeking potential mates.

How do females of *P. albopilosus* hunt? Females flew swiftly from the nesting area into vegetation surrounding the dune, where they were quickly lost from sight. There were few direct observations of female *P. albopilosus* hunting. Inferences on methods of hunting are

---

[2]Comparison of the proportion of bees to wasps was made using the statistic Chi Square at a significance level of $\alpha = 0.05$. The null hypothesis was that there is no difference in proportions of genera of bees and wasps used as prey as opposed to potential prey. The calculated statistic, $\chi^2 = 10.12$ is greater than the expected statistic, $\chi^2 = 3.84$. The null hypothesis is rejected, the proportions are not the same.

derived from examination of Table 5 and its comparison with Table 6.

In view of the prey captured I think that two different methods of hunting are employed. The first is to 'pounce on any apocritan that moves'. This would produce a wide spectrum of prey used and would not be biased toward a particular species or sex. A number of apocritans not commonly encountered in large numbers would be used.

A second method of prey capture may be to attack and capture male bees or wasps trailing the female beewolf. Males of many species of bees and wasps readily trail other insects which appear to be potential mates. Those who recognize the mistake before the beewolf detects them may survive. Male bees and wasps which are much larger or smaller than females of *P. albopilosus* may detect the error at greater distance; those whose females are of similar size and colour would likely continue pursuit and may possible grapple with the beewolf. It is not known if the female beewolf detects male bees and wasps at a distance or close up; observations are needed. It should be noted that the three species of prey captured in the greatest number were males of *Aphilanthops frigidus* (F. Smith), *Colletes* sp. and *Halictus rubicundus* Christ. Females of the three prey species approximate the size and appearance of female *P. albopilosus*. Neither the *A. frigidus* wasps nor the *Colletes* sp. and *H. rubicundus* bees were very abundant around the dunes.

Philanthus females are primarily visual hunters (Alcock 1974) which decide upon prey acceptability after contact (Armitage 1965). Females of most species of *Philanthus* documented in the literature

hunt on flowers and use mostly bees as prey (Armitage 1965, Evans 1966b, 1970, Reinhard 1922, Tinbergen 1935 and others). By inference via comparison of potential prey and prey selected, in conjunction with observations it may be hypothesized that, female *P. albopilosus* selected prey by: 1) use of vision in the initial finding of prey, but discriminating suitable prey from insects encountered occurs after contact was made (size, taxon and quality), 2) use of two methods of hunting, a) indiscriminate pouncing on flying insects (mostly apocritans) around the dune and, b) capturing males of apocritans pursuing them as potential mates and 3) searching for prey around the dune, but not on flowers as is common for females of other species of *Philanthus*.

The prey selected by female *P. albopilosus* (Empress dunes) is consistent with a population examined by Evans (1975) at Albany, New York, but inconsistent with the population examined by him at Roggen, Colorado. This suggests that there may be either a genetic basis, which is behaviourally manifested in either: 1) site of prey capture or, 2) acceptability of potential prey after contact has been made or, 3) the result of opportunism.

Change in prey selected, may have occurred as a result of populations of *P. albopilosus* becoming isolated in different refugia during the Wisconsin glaciation. In a northern refugium (Nebraska Sand Hills, see Section 8) changes in faunal composition occurred as a result of changing climate. This may have accounted for a shift in prey selection. A decreasing abundance and number of suitable species of bees, as prey, may have induced the eventual selection of a population of *P. albopilosus* which used sphecid wasps as a major

component of prey selected. Selection of sphecids over other groups of wasps may be in part, due to prevalence of dune nesting species with similar environmental tolerances, relative abundance around dunes and a suitable body size.

I postulate that the major evolutionary events occurred during the Wisconsin but the processes may still be acting on populations of *P. albopilosus* which are manifested in behavioural shifts which control various aspects of prey selection. The northern populations appear to have diverged, expanding the spectrum of prey taken, while the southern populations retain a narrow prey spectrum specializing on bees.

7. GEOGRAPHICAL DISTRIBUTION AND VARIATION

7.1 Known Range and Locality Data

Philanthus albopilosus is almost transcontinental in distribution with the most eastern known locality at Albany, New York (Evans 1975) and the western most at Hatton, Washington. The most northern locality is 175 km north of Empress at Rutland, Saskatchewan. It is doubtful that the range extends much further north. The southern known extreme is on Padre Island, Texas. Probably the range extends into central Mexico, but confirmation is required.

Localities of material studied are listed below. Numbers following locality names indicate the number of females examined followed by the number of males examined. Acronyms represent collections from which the material was borrowed.

Material examined:

CANADA. Alberta: Empress (11 km south), 31, 8; Medicine Hat, 6, 14, (CNC, UAS); Orion, 0, 2, (UAS). Manitoba: Aweme, 2, 8, (CNC, UCD); Harteny 0, 1, (SEM); Onah, 3, 0, (CNC). Saskatchewan: (see Empress, Alberta) Elbow, 5, 6, (CNC, UCD); Rutland, 3, 8, (CNC, UCD).

MEXICO. Chihuahua: Samalyuca, 0, 1, (UCD).

UNITED STATES. Arizona: Coconino County: Tuba City, 1, 0, (CUM); Navajo County: Hotenvilla, 1, 1, (UCD); Indian Wells (16 miles south), 1, 0, (UCD); Judito Trading Post, 1, 2, (UCD); Joseph City, 0, 1, (UCB); Kayenta (19 miles southwest), 2, 0, (CAS).

Colorado: Alamosa County: Great Sand Dunes National Monument, 0, 2, (CSU); Bent County: Hasty, 1, 1, (CSU); Prowers County: Carlton, 1, 3, (CSU); Lamar (10 miles west), 0, 2, (CSU); Weld County: Roggen, 9, 0, (CSU). Idaho (Strandtmann 1946). Iowa: Woodbury County: Sergeant Bluff, 1, 1, (USNM); Sioux City, 0, 1, (USNM). Illinois: Cook County: Chicago, 2, 5, (MCZ). Kansas: Kearny County: McKinney Lake, 0, 1, (MCZ); Stafford County: Salt Flats, 2, 4, (CUM, CNC, MCZ). Minnesota: Polk County: Muskoda, 0, 1, (CUM). Montana: 0, 2. Nebraska: Cumming County: West Point, 1, 2, (USNM). New Mexico: Dona Ana County: Las Cruces, 0, 2, (CAS, SEM); Otero County: White Sands National Monument, 0, 5, (MCZ, UCD); San Juan County: Shiprock (near), 0, 1, (USNM); Socorro County: La Joya Wild Life Preserve, 8, 10, (CSU, MCZ). New York: Albany County: Albany (Evans 1975). North Dakota: Billings County: Medora, 0, 1, (MCZ); Ransom County: Mcleod, 1, 1, (UCB), Sheldon, 2, 1, (CUM, MCZ); Richland County: Walcott (11 miles west), 1, 0, (UCD); Williams County: Williston, 1, 2, (MCZ). Ohio (Strandtmann 1946). South Dakota: Fall River County: Hotsprings, 1, 0, (MCZ). Texas: El Paso County: Fabens, 0, 2, (CAS, SEM); Hartly County: Romero, 2, 4, (SEM, UCD); Nueces County: Padre Island, 0, 1, (UCD); Ward County: Monahans State Park, 10, 22 (CSU, MCZ). Utah: Juab County: Eureka, 0, 1, (UCB); Utah County: Utah Lake, 0, 1, (CUM). Washington: Adams County: Hatton, 0, 1, (USNM).

In total 227 specimens were examined, 96 females and 131 males. Positions of localities are mapped in Figure 4. Dotted lines encompassing groups of points define groups of populations which were united and treated as a single population, to increase sample sizes for statistical purposes. Numbers associated with each area, are used

Figure 4. Distribution of *Philanthus albopilosus.*

Numbers shown are used in the text to refer to the localities enclosed by the dotted line. The dark race of *P. albopilosus* occurs north of the dashed line, the light race to the south and Area 1, is not assigned to a race group.

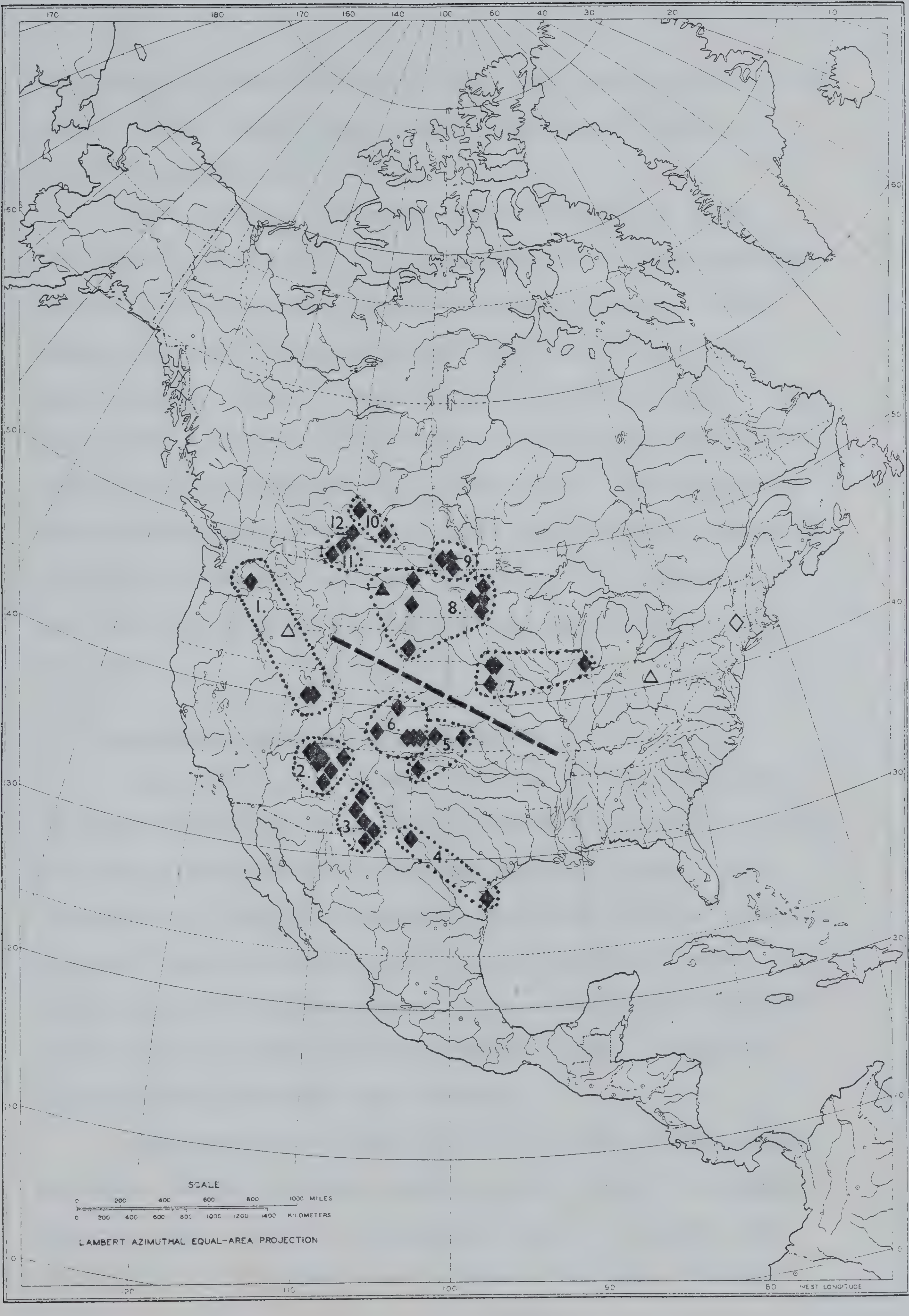
Symbols used:

◆ locality, specimens seen

◇ locality, specimens not seen

▲ state record, specimens seen

△ state record, specimens not seen


1.
2.
3.
4
5
6
7
8.
9
10
11
12.
SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE

in the text in reference to these areas. An attempt was made to group populations into natural groups, using geographical barriers (if present) as boundaries.

Most localities are in semi-arid to arid regions of the Great Plains with clusters in the desert regions. A range extension appears to follow the arid interior into the Great Basin. Three eastern localities: Chicago, Illinois; Ohio and Albany, New York appear somewhat disjunct. These localities may not be unusual: on a gross level of analysis the beewolves are not found in regions where annual precipitation exceeds 91.5 cm (36 inches). Moisture may be affecting presence or absence of suitable habitats rather than having a direct influence on the species. Activities by man permit colonization of disturbed sites such as sand and gravel pits and road cuts.

7.2 Geographical Variation in Colour Pattern

Interpretations of species limits for many *Philanthus* wasps, is based on maculation and punctation patterns in the adults. A group of closely related species of *Philanthus* were once thought to be subspecies of *P. politus*. Recognition was in part based on coloration of tibia, femora, and punctation and shape of metanotal lamina. In another species *P. zebratus* several forms once recognized as distinct species have been united and given subspecies status. Diagnostic characters were maculations and punctures.

After examining specimens of *P. albopilosus*, it appeared that there were recognizable groups based on colour patterns. A compound character index was used to quantify the data and the results are shown in Figure 5 for females and in Figure 6 for males. To give

Figure 5. Compound character index values for females of *Philanthus albopilosus*.

Area numbers refer to those illustrated in Figure 4.

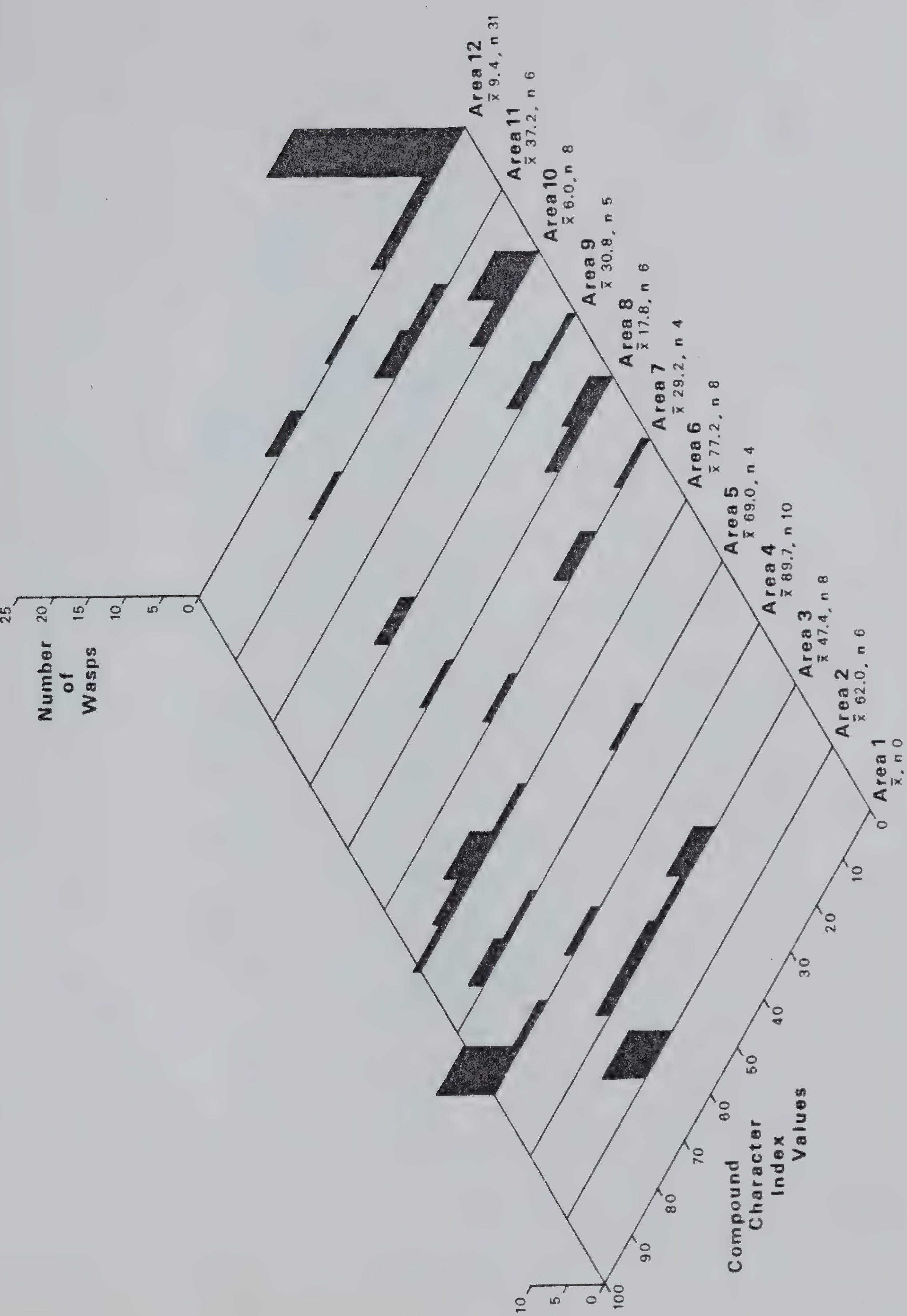
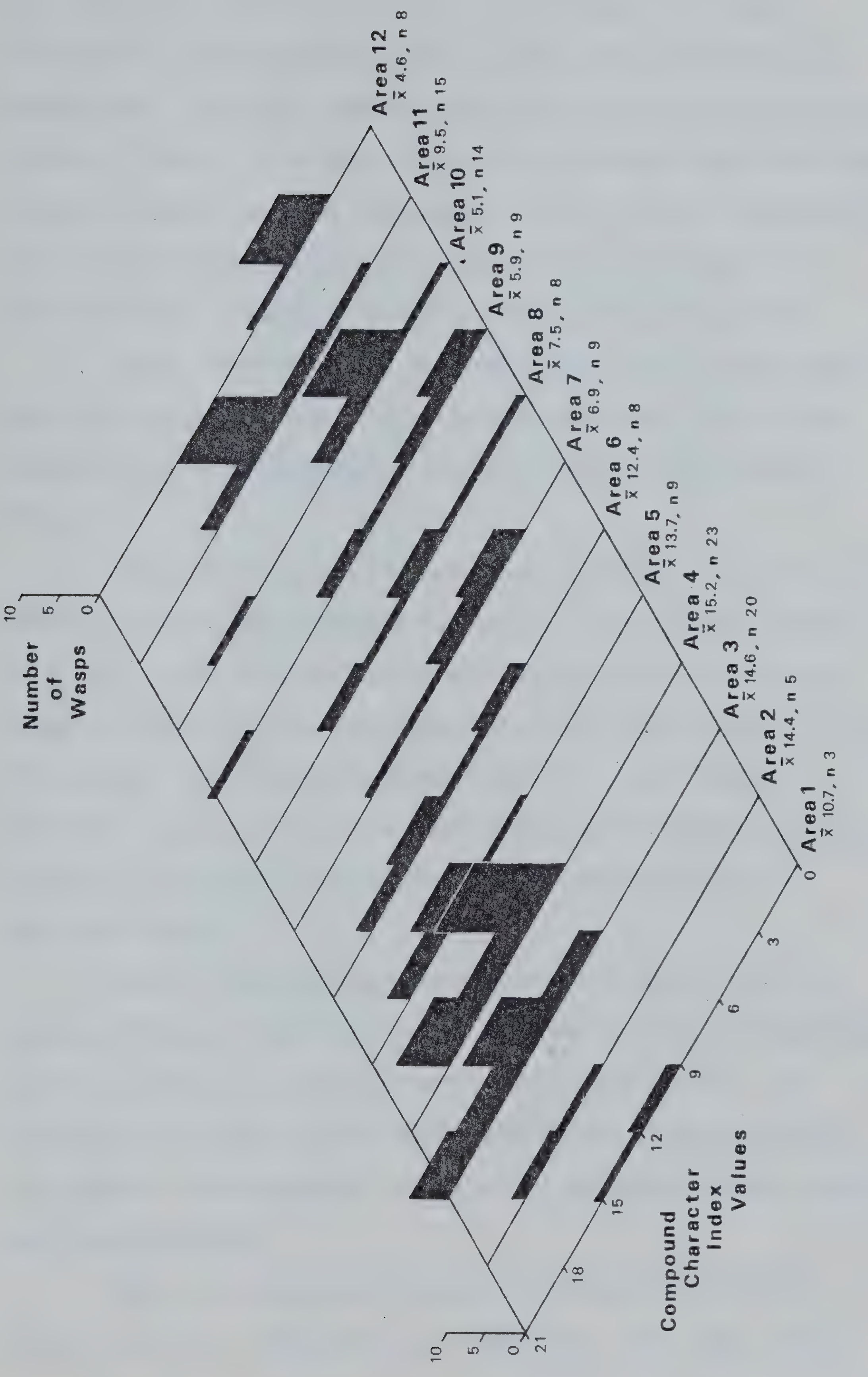

Number of Wasps
25
20
15
10
5
0
Area 12 x̄ 9.4, n 31
Area 11 x̄ 37.2, n 6
Area 10 x̄ 6.0, n 8
Area 9 x̄ 30.8, n 5
Area 8 x̄ 17.8, n 6
Area 7 x̄ 29.2, n 4
Area 6 x̄ 77.2, n 8
Area 5 x̄ 69.0, n 4
Area 4 x̄ 89.7, n 10
Area 3 x̄ 47.4, n 8
Area 2 x̄ 62.0, n 6
Area 1 x̄, n 0
0
10
20
30
40
50
60
70
80
90
100
Compound Character Index Values
10
5
0

Figure 6. Compound character index values for males of *Philanthus albopilosus*.

Area numbers refer to those illustrated in Figure 4.


Number of Wasps
10
5
0
Area 12 x̄ 4.6, n 8
Area 11 x̄ 9.5, n 15
Area 10 x̄ 5.1, n 14
Area 9 x̄ 5.9, n 9
Area 8 x̄ 7.5, n 8
Area 7 x̄ 6.9, n 9
Area 6 x̄ 12.4, n 8
Area 5 x̄ 13.7, n 9
Area 4 x̄ 15.2, n 23
Area 3 x̄ 14.6, n 20
Area 2 x̄ 14.4, n 5
Area 1 x̄ 10.7, n 3
0
3
6
9
12
15
18
21
Compound Character Index Values

some perspective to the index values used, Figure 7 a, b and d illustrate a dark northern female; not all of the characters are illustrated. The total compound character index value for the specimen is zero. Figure 8 a, b and d illustrate a southern female which has a total compound character index value of 93. Figure 9 illustrates the typical frontal maculation of the head and an abdomen of a northern male. This male received a total index value of four.

Sample sizes from many individual localities were too small and were pooled into more or less natural geographic units. Area numbers refer to the geographic areas enclosed by dashed lines in Figure 4.

Figure 4 represents the variation in maculation patterns in females; no data were available for Area 1. In the north (Areas 7, 8, 9, 10, 11 and 12) index values are concentrated toward the low range, indicating populations comprised of dark individuals. Most of the specimens received index values below 30. A few maculate specimens were present but the index values did not exceed 70 units. Figure 7 illustrates a dark northern female and the face of a maculated female.

Samples from more southern localities (Areas 4, 5 and 6) contained females which had extreme expansion of the yellow markings and few specimens were assigned index values less than 70. No populations are known to have intermediate index values and occur as geographic intermediates. In Figure 8, two females of the yellow race are illustrated.

Females from mountain regions of southern United States (Area 2 and 3) are intermediate in coloration, with index values

Figure 7. Typical and maculated specimens of female *Philanthus albopilosus* of the northern race.

Figures 7a, 7b and 7d head, thorax and abdomen of dark Empress, Alberta specimen. Figure 7c, head of maculated specimen of dark race at Medicine Hat, Alberta.

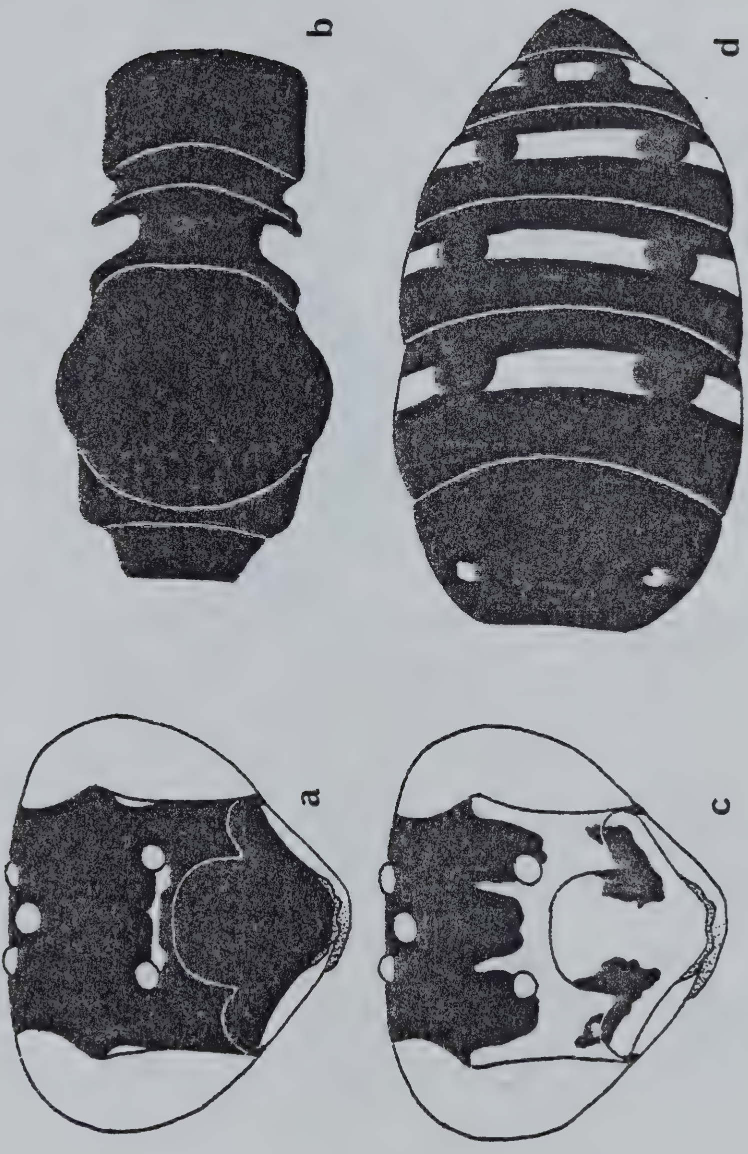

a
b
c
d

Figure 8. Typical specimens of females of the light race of *Philanthus albopilosus*.

Figures 8a, 8b and 8d, head thorax and abdomen of specimen from Monahans, Texas. Figure 8c, head of specimen from Roggen, Colorado.

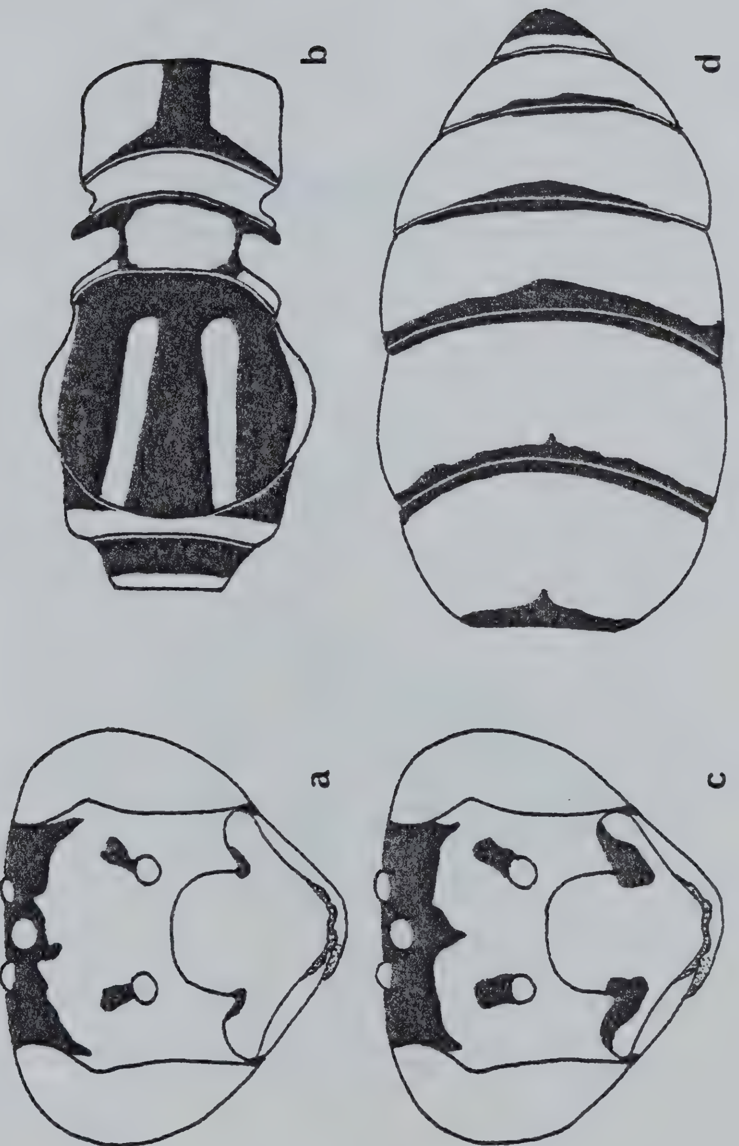
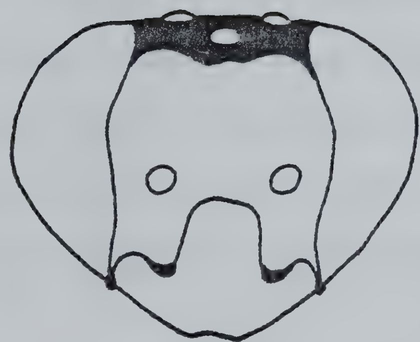
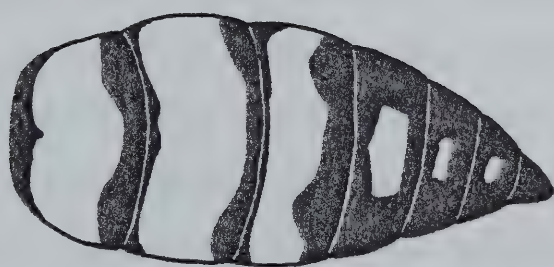

a
b
c
d

Figure 9. Head and abdomen of male *Philanthus albopilosus* wasp from Empress, Alberta showing typical maculation pattern for most males.



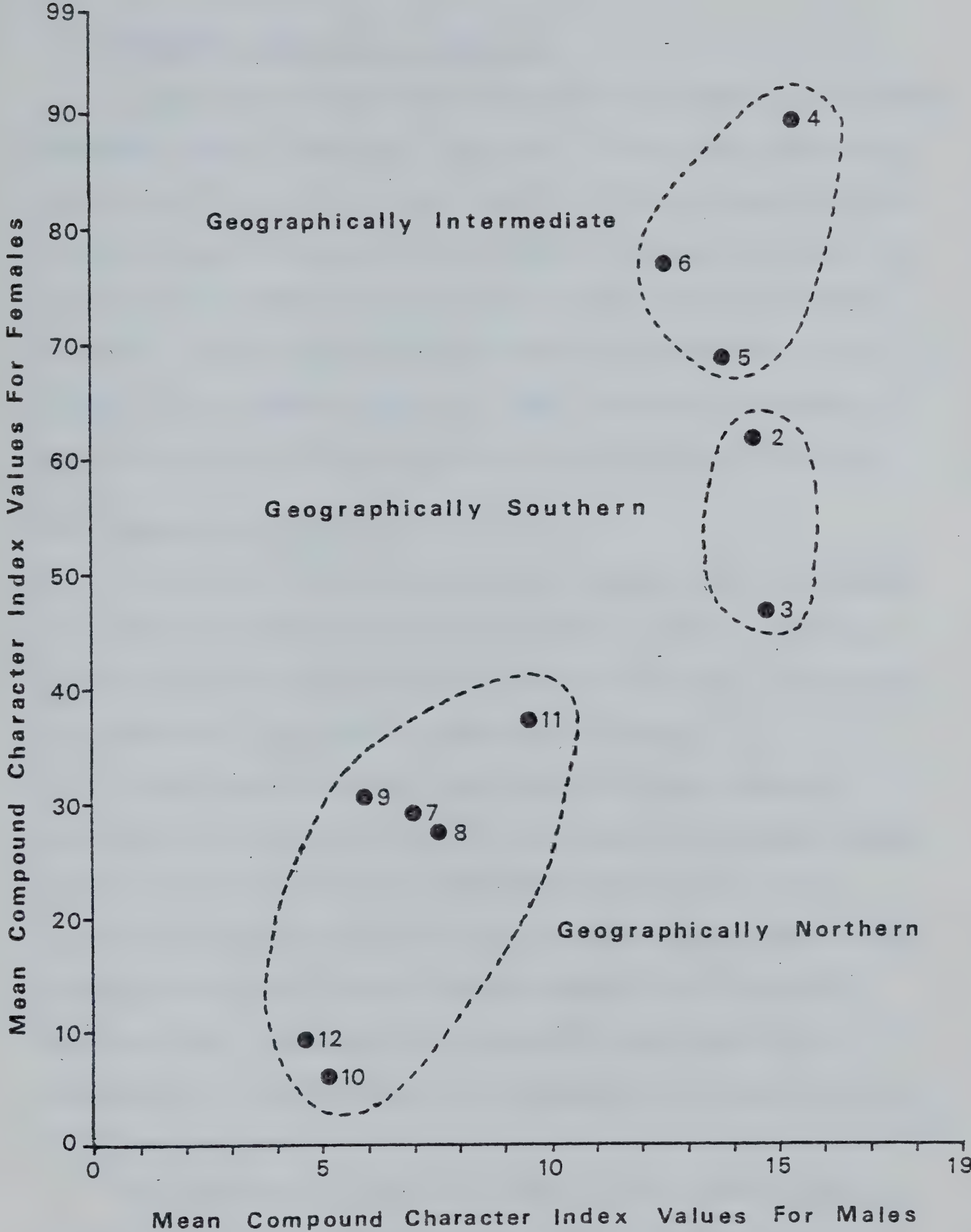


between 30 and 70. These groups are the most geographically distant populations from those in the northern areas.

Males of *P. albopilosus* also exhibit some trends in coloration (Figure 6) but these are not as distinctive. The northern populations in Areas 7, 8, 9, 10, 11 and 12 had individuals tending to be darker, as reflected in lower index values. Males from the southern areas (Areas 2, 3, 4, 5 and 6) tend to be pale, which reflected in higher index values. There is not a discrete break in the index values but a trend to shift to darker forms in the north and lighter forms in the south. The sample from Area 1 was too small to show trends: males were of intermediate coloration. Figure 9 shows a northern male.

Index values for each area were averaged, and a plot of the female index values versus the male index values is presented in Figure 10. If the points formed a random scatter, I would assume that there is no evidence to support geographic races. The points form loose clusters: the northern groups separate together, in contrast to the southwestern populations and the geographically intermediate populations. The points illustrate a break in variation, with the largest break occurring between the geographically intermediate group and the northern group. The phenotypic intermediate groups are the extreme southwestern which may grade into the geographically intermediate group. The results should be used with caution as some sample sizes are small and hence may not give an accurate representation of variation in the respective populations. Area 1 was not plotted because of absence of female index values.

Figure 10. Compound character index value comparisons of means for colour variation in wasps of *Philanthus albopilosus*. Numbers refer to areas illustrated in Figure 4.


Geographically Intermediate
Geographically Southern
Geographically Northern
Mean Compound Character Index Values For Females
Mean Compound Character Index Values For Males
0
10
20
30
40
50
60
70
80
90
99
0
5
10
15
19
4
6
5
2
3
11
9
7
8
12
10

7.3 Geographical Variation in Behaviour

Data on ethological variation is harder to gather as individual populations must be observed in the field. In the three populations which have been observed, several aspects of the life history should be noted. In northern populations (Empress, Alberta and Albany, New York) burrow galleries are shallow, prey selection is broad (number of species) and includes wasps (parasitoids and aculeates) as well as bees. In a southern population, Roggen, Colorado, the burrow is deep and prey selection is restricted to few species of bees, only.

7.4 Taxonomic Interpretation

The beewolf species *P. albopilosus* includes two major groups of populations, based primarily on coloration patterns. Additional support is given by certain aspects of the life history, burrow depth, prey specificity and number of generations per year.

Populations of the dark form appear to form a cohesive geographic unit across the northern United States and southern Canada (Areas 7, 8, 9, 10, 11 and 12). Many population samples differ slightly from samples collected in more or less adjacent areas. Such differences may be due in part to the "founder effect" (MacArthur and Wilson 1967), associated with invasion of new areas by few individuals. No geographical barriers are apparent between localities of the northern race.

The southern light form is a slightly less coherent grouping. In Areas 2 and 3, an intermediate colour form is present, which is partly isolated by mountain divide systems from populations of the

extreme yellow form found in Areas 4, 5 and 6.

In interpreting the data it appears that there has been a break in gene flow between the northern populations and the southern populations (Figure 10) for an extended period of time (probably the Wisconsin glaciation). At present gene flow is interrupted between some populations in the southern race by physiographic barriers. On the Great Plains gene flow appears restricted between northern areas (7 and 8) and southern areas (5 and 6). No populations of intermediate coloration were found between these areas. There is little reason to doubt that a highly vagile insect like a beewolf should not disperse and introgress into other populations.

Character displacement may occur between ecologically similar races which do not freely interbreed. Lack of a physiographic boundary separating the races would indicate that contact has recently occurred (Vuilleumier 1971). The character displacement model would be applicable only if areas of abuttment or narrow overlap of ranges were involved, but with *P. albopilosus* Area 4 populations do not come in contact with the northern race.

Working with the premise that the races have come into recent contact implies a boundary was present at some phase in the species history. Area 4 populations may be relatively recent arrivals being derived from the yellow populations further to the north which are in contact or abuttment with the northern race. Origin from Areas 2 or 3 is less likely because of mountain divide systems. A north-south movement on the Great Plains is more probable because of relative lack of geographic barriers.

The major isolating event separating the northern and southern races was probably the Wisconsin glaciation. Isolation of the lineages would have occurred before the zenith, probably in the late Sangomon interstadial. This would place the dichotomy at about 60,000+ years B.P. Whitehead (1972) suggested that speciation occurs at a rate of about one dichotomy per 3,000,000 years. On the basis of this hypothesis, races of *P. albopilosus* have not been isolated long enough, to have evolved into good species.

Regardless of what actually happened in the past, populations of *P. albopilosus* may be arranged in definable races on the basis of phenotypic variation correlated to geographic regions and for a few populations further evidence is supplied by aspects of life history and behaviour. Many authors have considered the species subspecies concept and each has a slightly different idea of what the species-subspecies limits should be; some are for recognition, others are against. I prefer the argument given by Willis (1967) ". . . if subspecies reflect to some degree the actual pattern of variation, as well as being convenient 'handles' for reference, their value seems sufficient to justify their recognition". I do not wish to describe a new taxon now so I will simply refer to the races as the dark or northern race (Areas 7, 8, 9, 10, 11 and 12) and the light or southern race (Areas 2, 3, 4, 5 and 6). Area 1 populations are unplaced.

8. SYNTHESIS

Examination of populations of *P. albopilosus* provides information in two basic areas: that which pertains to interspecific and intraspecific interactions. The first part of the Synthesis (8.1) deal with intraspecific interactions in an evolutionary perspective. In the last part (8.2) interspecific relationships with other species of *Philanthus* and digger wasps are noted.

8.1 Toward a Synthesis of Post Pleistocene Dispersal of *P. albopilosus*

8.1.1 Antecedents

The appearance of races of *P. albopilosus* indicated fragmentation of the ancestral range of the species and hence isolation of populations for an extended period of time, possibly during the Pleistocene. It is the intent in this section to relate the divergence in structure and behaviour to the events which might have been causative or antecedent. The major events of Pleistocene history of North America were documented by Flint (1971) and aspects of the glacial history of the Great Plains were documented in Dort and Jones (1970) and Wendorf and Hester (1975).

Due to similarities between the races, a time scale may be superimposed which will correlate the events with a relatively recent origin. The Sangamon interstadial between the Illinoian and Wisconsin glaciations will serve as a starting point. Relatively little attention has been directed to reconstruction of climates and biotic

associations of the earlier glacial phases. Most of the attention has been focused on reconstruction of climate and biotic associations of the Wisconsin to recent. Flint (1971) discusses briefly probable conditions during the Sangamon, which range from arid in the southwest to cool and moist. I interpret this as implying that the climate may be comparable to today's, with similar plant biomes. Dune habitats would have been present in many areas where they are currently found.

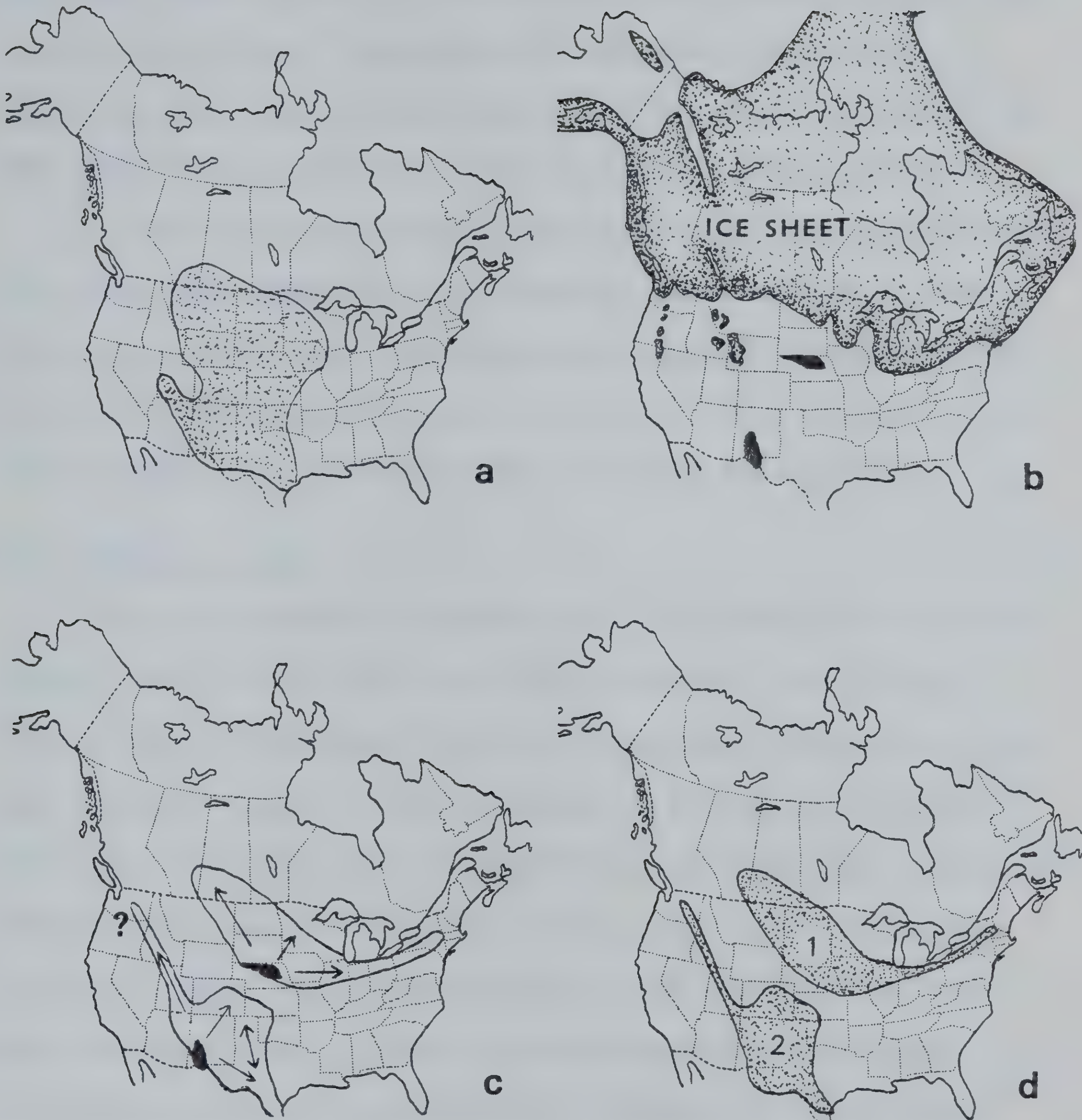
The ancestral taxon of *P. albopilosus* was probably similar in appearance to individuals found in Areas 2 and 3. Females would be about the same size, and nest in dune and blowout habitats. Judging from prey preference in other species of *Philanthus* and prey preference in the southern populations, halictid bees would be the primary prey with other bees comprising a lesser proportion. Burrows may have been deep as a result of competition for nesting space or an adaptive response to high ground temperatures.

Distribution of the ancestral stock was probably across the Great Plains, extending north into Canada, Figure 11. It is assumed that the beewolves did not occupy sand dunes in the northern Great Basin, or if they did, the populations went extinct during the Wisconsin glaciation.

8.1.2 Effect of the Wisconsin Glaciation

Toward the end of the Sangamon interglacial the climate began to cool (about 70,000 B.P.); deterioration continued giving rise to the Wisconsin glaciation (from 55,000 B.P. to 10,000 B.P.). Cool wet conditions induced reforestation of much of the Great Plains. Increased moisture also caused reduction of sand dune habitats as ground cover increased.

Figure 11. Distribution patterns of *Philanthus albopilosus* through time, a) 70,000 B.P. hypothetical range of ancestral stock, b) *Ca.* 17,000 B.P. geographic isolation of ancestral stock at the zenith of the Wisconsin, c) *Ca.* 7,000 B.P. expansion of ranges from refugium, d) recent distribution of (1) dark race and (2) light race.


ICE SHEET
a
b
?
c
1
2
d

However, in contrast, in large dune fields, porosity of the sand would induce aridity by exceptionally good ground drainage; thus blowouts may develop. Populations of *P. albopilosus* (*s.l*) in association with large dune fields may have survived. Populations on small dune systems would have a high probability of going extinct.

Toward the end of the Wisconsin glaciation climate ameliorated, life zones moved north and up in elevation. Many stabilized dunes would become active permitting geographic dispersal. Maximal aridity occurred during the Hypsithermal, also maximal rates of dispersal may have occurred due to increased dune and blowout development.

8.1.3 Refugial Areas

In the southwestern United States, arid regions may have been present during the Wisconsin glaciation, permitting dune fields to remain active. Pleistocene floras of the American southwest have not been accurately depicted possibly because of the extreme topographic diversity. Life Zones may have shifted down the mountains, but may not have been depressed to the extent that the valley flora was totally replaced. Intense solar radiation in the lower latitudes may have had a buffering effect on south-facing slopes and valley bottoms. The American southwest is proposed as a refugium for the southern race of *P. albopilosus*.

To propose a northern refugium a suitable area must be present during the Wisconsin glaciation. Examining the map compiled by Thorp *et al.* (1952) of Pleistocene eolian deposits, very few suitable sites are available east of the Mississippi River which could serve as refugia. Most of eastern North America would have been cloaked in a continuous forest (Ross 1970, Martin 1958, Frenzel 1973, and others).

On the Great Plains, several sand dune areas exhibit features indicating that some dunes were active during various portions of the Wisconsin glaciation. Smith (1965) demonstrated that there were several periods of dune building on the Nebraska Sand Hills, as evidenced by past movement of stabilized dunes. Northerly winds probably blowing off the ice mass were the prevailing winds. At present the prevailing winds blow from the west. The large dune area may have served as a refugium for some of the sand dwelling organisms which were able to adapt to a cooler climate.

A refugium near the ice front is not a new idea. Latitudinal gradients of the vegetation formations may have been greatly compressed (Ross 1970). Willis (1967) proposed survival of at least five species of tiger beetles (*Cicindelida*: Cicindelidae) in the vicinity of Lincoln, Nebraska during the Pleistocene. I suggest that the ancestral stock of the northern race of *P. albopilosus* survived during the Wisconsin glacial stage of Pleistocene in a refugium in the vicinity of the Nebraska Sand Hills.

8.1.4 Differentiation in the Refugium

Adaptation to a cooler climate during the Wisconsin glaciation by populations in the northern refugium may have been the major evolutionary reason for differentiation. Females of the northern race are dark: this may be a functional adaptation for absorbing radiant heat, which may prolong the length of the time per day in which they could hunt. Males may not require as much darkening, as they could restrict their activities to the hot microenvironment of the sand dune surface.

Shallow burrows may be a response to cool ground temperatures. Cells close to the surface would warm sooner and experience warmer temperatures permitting rapid development in an area with a shorter growing season.

A change in prey specificity may be a response to a reduction in number and species of halictid bees available during the Wisconsin. Alternate prey species would be incorporated from other groups of Apocrita.

8.1.5 Post-Wisconsin Dispersal

Following the Wisconsin glaciation, climate ameliorated, and many sand dunes developed and older ones become reactivated. Figure 11c illustrates proposed dispersal patterns for *P. albopilosus* from the refugia.

Expansion of the southern race onto the Great Plains should have seen rampant colonization of most of the prairie sand dunes. Some factor appears to have restricted dispersal. The light race has expanded east and northward on the Great Plains. Expansion of range appears to have been limited by the presence of the dark race in the north. The rare occurrence of *P. albopilosus* in the Great Basin may be the result of relatively recent post-Pleistocene dispersal.

The very pale form on the Great Plains is somewhat of a puzzle: character displacement was suggested in section 7.4, but this does not adequately explain the populations found in Area 4, unless, there is considerable gene flow between the populations on the plains. Mountain barriers would buffer populations found in Areas 2 and 3 from an influx of extreme pale forms.

Present distribution of the northern race is the result of post-Pleistocene dispersal into new dune habitats. An eastern and northwestern expansion of range has occurred. Southward expansion may have been blocked by the presence of the southern race. There may be enough behavioural differences to reduce the tendency for the groups to hybridize.

It is not known if limited introgressive hybridization is occurring. A small percentage of the northern populations contain well marked individuals. These may be the result of reversed natural selection toward a form with typical warning coloration pattern, or they may represent remnants of the ancestral gene pool. In the southern populations almost all specimens examined can be easily distinguished from the northern race. One Colorado female was intermediate between normal southern and well marked northern forms. Other dark southern specimens were present but clearly not approaching an intermediate condition. The above discussion is primarily based on variation in the females; trends are present in males but are more conservative.

8.2 Characterization of *P. albopilosus*

Some evolutionary adaptations exhibited by *P. albopilosus* converge on those seen in other digger wasps. Development of false burrows originated from nest parasite pressures, which are reported as intense in open environments. Orientation to the nest is difficult for females, as landmarks near the nest may change in an unstable dune environment. Use of distant landmarks is important, but fixation to these requires seeing the nest site while orienting and keeping nest

parasites out. False burrows may serve both of these functions.

Short occupancy time of the nest as compared to other species of *Philanthus* may be due to the friable nature of the soil. Little time is spent digging in comparison to species which dig in hard soils. Few cells per nest would be a function of the ephemeral occupancy coupled with slow provisioning. A relatively long adult life span, nest location in areas devoid of vegetation and anti-parasite nest building behaviours may reduce selection pressures for the production of large numbers of offspring ("K" selection).

Reduction in the number of generations per year in northern populations is probably a result of shorter growing seasons either presently or during the species evolutionary history.

The relative absence of other species of *Philanthus* on the Empress dunes indicates the specialization of *P. albopilosus* for life on sand dunes.

These facets of the life history serve as a characterization of the species *P. albopilosus* as a whole. This also serves in part, as a start in the characterization of the northern fauna of *Philanthus*.

9. HYPOTHESES AND FUTURE STUDIES

Many ideas have been brought forward in this study, some of which deserve further study.

False burrows have been proposed as an aid in orientation. How might this idea be tested? Repetition of some of van Iersel's (1964) experiments may be appropriate to determine if distant land marks are used. Testing whether the false burrows are used would involve moving them without disturbing the wasp before, during or after the orientation flight. The result should provide insights into the degree of importance in relation to orientation.

Predictions can be made on the colour form expected to occur in the Great Basin. Predictions may be made regarding aspects of the beewolf's behaviour. I predict that females of the Great Basin populations will be of a light colour form. I also predict that females of the light southern race will dig deep nests, and hunt mostly bees, the dark northern races will have shallow nests and hunt a wide range of apocritan Hymenoptera. To test these predictions collection and observation of many additional populations will be required. Accumulation of these data will enable further testing of the hypothesis that the taxon *P. albopilosus* is composed of two distinct subspecies.

Knowing the post-Pleistocene pattern of dispersal for *P. albopilosus* may help in understanding the source of the prairie and dune fauna found in Alberta and other prairie provinces. The

proposal of a northern refugium permits the investigation of other organisms, providing a guide for seeking further evidence, to support or to oppose the hypothesis.

REFERENCES

REFERENCES

Alberta Environment, 1975. Climate of Alberta, tables of temperature, precipitation and sunshine. 90 pp.

Alcock, J. 1974. The behaviour of *Philanthus crabroniformis* (Hymenoptera: Sphecidae). Journal of Zoology. London 1973: 233-246.

Alcock, J. 1975. Territorial behaviour by males of *Philanthus multimaculatus* (Hymenoptera: Sphecidae) with a review of territoriality in male sphecids. Animal Behaviour 23: 889-895.

Armitage, K.B. 1965. Notes on the biology of *Philanthus bicinctus* (Hymenoptera: Sphecidae). Journal of the Kansas Entomological Society 38: 89-100.

Amadon, D. and L.L. Short. 1976. Treatment of subspecies approaching species status. Systematic Zoology 25: 161-167.

Ashwell, I.Y. 1966. Glacial control of wind and of soil erosion in Iceland. Annals of the Association of American Geographers 56: 529-540.

Bergstrom, R.E. (Ed.). 1968. The Quaternary of Illinois. University of Illinois, College of Agriculture, Special Publication No. 14, 179 pp.

Bohart, G.E. 1954. Honeybees attacked at their hive entrance by the wasp *Philanthus flavifrons* Cresson. Proceedings of the Entomological Society of Washington 56: 26-27.

Bohart, R.M. 1972. New North American *Philanthus*. Proceedings of the Entomological Society of Washington 74: 397-403.

Bohart, R.M. and E.E. Grissell. 1975. California wasps of the subfamily Philanthinae (Hymenoptera: Sphecidae). Bulletin of the California Insect Survey, Vol. 19, 92 pp.

Bohart, R.M. and A.S. Menke. 1976. Sphecid wasps of the world, a generic revision. University of California Press 695 pp.

Bryson, R.A. and W.M. Windland. 1967. Tentative climatic patterns for some late glacial episodes in Central North America pp. 279-297. *In* Mayer-Oakes, W.J. (Editor), Life, land and water. University of Manitoba Press, Winnipeg.

Cazier, M.A. and M.A. Mortenson. 1965. Studies on the bionomics of the sphecoid wasps II. *Philanthus gibbosus* (Fabricius) and *Philanthus anna* Dunning (Hymenoptera: Sphecidae). Bulletin of the Southern California Academy of Sciences 64: 171-206.

Chadwick, H.W. and P.D. Dalke. 1965. Plant succession on dune sands in Fremont County Idaho. Ecology 46: 765-780.

Chapman, R.N., C.E. Mickel, J.R. Parker, G.E. Miller, and E.G. Kelly. 1926. Studies in the ecology of sand dune insects. Ecology 7: 416-426.

Cotton, M.J. 1967. Aspects of the ecology of sand dune arthropods. Entomologist 100: 157-165.

Coupland, R.T. 1950. Ecology of the mixed prairie in Canada. Ecological Monographs 20: 271-315.

Dort, W. and J.K. Jones (Ed.). 1970. Pleistocene and recent environments of the Central Great Plains. Department of Geology, University of Kansas Special Publication 3, University of Kansas Press.

Dowding, E.S. 1929. The vegetation of Alberta III. The sand hill areas of central Alberta with particular reference to the ecology of *Arthrobium americanum* Nutt. Journal of Ecology 17: 82-105.

Downes, J.A. 1964. Arctic insects and their environment. The Canadian Entomologist 96: 279-307.

Edmunds, F.H. 1944. Geology and its relationship to soils in Saskatchewan pp. 219-249. In Mitchell, J., H.C. Moss and J.S. Clayton. Soil survey of Saskatchewan from township 1 to 48 inclusive. Soil Report No. 12. Saskatoon, Saskatchewan.

Edmunds, F.H. 1962. Recession of Wisconsin Glacier from central Saskatchewan. Saskatchewan Department of Mineral Resources, Report No. 67.

Evans, H.E. 1955. *Philanthus sanbornii* Cresson as a predator on honeybees. Bulletin of the Brooklyn Entomological Society 50: 47.

Evans, H.E. 1964a. Notes on the nesting behaviour of *Philanthus lepidus* Cresson (Hymenoptera: Sphecidae). Psyche 71: 142-149.

Evans, H.E. 1964b. The accessory burrows of digger wasps. Science 152: 465-471.

Evans, H.E. 1966a. The comparative ethology and evolution of the sand wasps. Cambridge, Harvard University Press pp. 526.

Evans, H.E. 1966b. Nests and prey of two species of *Philanthus* in Jackson Hole, Wyoming (Hymenoptera: Sphecidae). Great Basin Naturalist 26: 35-40.

Evans, H.E. 1966c. The behavior of solitary wasps. Annual Review of Entomology 11: 123-154.

Evans, H.E. 1970. Ecological-behavioral studies of the wasps of Jackson Hole, Wyoming. Bulletin of the Museum of Comparative Zoology 140: 451-511.

Evans, H.E. 1973. Burrow sharing and nest transfer in the digger wasp *Philanthus gibbosus* (Fabricius). Animal Behaviour 21: 302-308.

Evans, H.E. 1975. Nesting behavior of *Philanthus albopilosus* with comparisons between two widely separated populations. Annals of the Entomological Society of America 68: 888-892.

Evans, H.E. and C.S. Lin. 1959. Biological observations on digger wasps of the genus *Philanthus* (Hymenoptera: Sphecidae). Wasmann Journal of Biology 17: 115-132.

Evans, H.E. and R.W. Matthews. 1975. The sand wasps of Australia. Scientific American 233(6): 108-115.

Flint, R.F. 1971. Glacial and quaternary geology. J. Wiley and Sons Inc. 892 pp.

Frenzel, B. 1973. Climatic fluctuations of the Ice Ages. The Press of Western Reserve University, Cleveland and London. 306 pp.

Freitag, R. 1965. A revision of the North American species of the *Cicindela maritima* group with a study of hybridization between *Cicindela duodecimguttata* and *oregona*. Quaestiones Entomologicae 1: 87-107.

Frisch, K. von. 1953. The dancing bees. Harvest books, New York. pp. 182.

Gressitt, J.L. 1958. Zoogeography of insects. Annual Review of Entomology 3: 207-230.

Holling, C.S. 1964. The analysis of complex population processes. The Canadian Entomologist 96: 335-347.

Howden, H.F. 1963. Speculations on some beetles, barriers and climates during the Pleistocene and Prepleistocene periods in some nonglaciated portions of North America. Systematic Zoology 12: 178-201.

Hubbs, C.L. 1958. Zoogeography. Pub. #51 of American Association for the Advancement of Science, Washington, D.C.

Hulett, G.K., R.T. Coupland and R.L. Dix. 1966. The vegetation of dune sand areas within the grassland region of Saskatchewan. Canadian Journal of Botany 44: 1307-1331.

Iersel, J.J.A. van. 1964. Orientation in the digger wasp *Bembix rostrata*. Animal Behaviour Supplement 1: 145-162.

Iwata, K. 1976. Evolution of instinct, comparative ethology of Hymenoptera. Amerind Publishing Co., New Delhi 535 pp.

Klassen, R.W. 1972. Wisconsin events and the Assiniboine and Qu'Appelle valley of Manitoba and Saskatchewan. Canadian Journal of Earth Sciences 9: 554-560.

Krombein, K.V. 1936. Biological notes on some solitary wasps (Hymenoptera: Sphecidae). Entomological News 47: 93-99.

Longley, R.W. 1977. Climatic change as it affects Alberta and the other prairie provinces. Alberta Environment Research Secretariat, 33 pp.

Lorenz, K. 1967. Evolution and Modification of Behavior. University of Chicago Press, 121 pp.

Löve, D. 1959. The postglacial development of the flora of Manitoba: a discussion. Canadian Journal of Botany 37: 547-585.

MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, 203 pp.

Malyshev, S.I. 1968. Genesis of the Hymenoptera and the phases of their evolution. Richard Clay Ltd., Bungay, Suffolk, 319 pp.

Martin, P.S. 1958. Pleistocene ecology and biogeography of North America. *In* Hubbs 1958, p. 375-470.

Mengel, R.M. 1970. The North American central plains as an isolating agent in bird speciation. *In* Dort and Jones 1970, p. 279-340.

Mitchell, J., H.C. Moss and J.S. Clayton. 1947. Soil survey of southern Saskatchewan, from township 1 to 48 inclusive, soil survey report No. 12. University of Saskatchewan College of Agriculture.

Mitchell, T.B. 1960. Bees of the eastern United States, Volume 1. North Carolina Agriculture Experimental Station, Technical Bulletin, No. 141.

Mitchell, T.B. 1962. Bees of the eastern United States, Volume 2. North Carolina Agriculture Experimental Station, Technical Bulletin, No. 152.

Peckham, G.W. and E.G. Peckham. 1905. Wasps, social and solitary. Houghton Mifflin and Co., New York, 311 pp.

Powell, J.A. and J.A. Chemsak. 1959. Some biological observations on *Philanthus politus pacificus* Cresson (Hymenoptera: Sphecidae). Journal of the Kansas Entomological Society 32: 115-120.

Priest, V.K. 1968. Quaternary geology of Canada, pp. 676-764. *In* Douglas, R.J.W. (Ed.) 1968. Geology and economic minerals of Canada. Geological Survey of Canada, Economic Geology, Report No. 1. Queens Printer, Ottawa 838 pp.

Ranwell, D.S. 1972. Ecology of salt marshes and sand dunes. Chapman and Hall, London 258 pp.

Rau, P. and N. Rau. 1918. Wasp studies afield. Princeton University Press, Princeton, New Jersey 372 pp.

Reinhard, E.G. 1924. The life history and habits of the solitary wasp *Philanthus gibbosus*. Annual Report Smithsonian Institution, 1922: 363-376.

Ross, H.E. 1970. The ecological history of the Great Plains, evidence from grassland insects. *In* Dort and Jones 1970, pp. 225-240.

Simpson, G.G. 1953. The major features of evolution. Columbia University Press, New York 434 pp.

Smith, H.T.U. 1938. Quaternary dune building in central Kansas. Proceedings of the Geological Society of America 1937: p. 115.

Smith, H.T.U. 1965. Dune morphology and chronology in central and western Nebraska. Journal of Geology 73: 557-578.

Sneath, P.H.A. and R.R. Sokal. 1973. Numerical taxonomy, the principles and practice of numerical classification. W.H. Freeman and Company, San Fransico 573 pp.

Strandtmann, R.W. 1946. A review of the North American species of *Philanthus* north of Mexico. Ohio State University Press, 126 pp.

Strickland, E.H. 1947. An annotated list of the wasps of Alberta. The Canadian Entomologist 79: 121-130.

Stroud, C.P. 1950. A survey of the insects of White Sands National Monument, Tularosa Basin, New Mexico. American Midland Naturalist 44: 659-677.

Summers, G.W. and W.S. Peters. 1973. Basic statistics in business and economics. Wadsworth Publishing Company, Inc. Belmont, California 445 pp.

Thorp, J., H.T.U. Smith, *et al.* 1952. Pleistocene eolian deposits of the United States and parts of Canada. Geological Society of America, map, scale 1: 2,500,000.

*Tinbergen, N. 1932. Über die Orientierung des Bienenwolfes (*Philanthus triangulum* Fabr.). Z. Vergleich. Physiol. 16: 305.

*Tinbergen, N. 1935. Über die Orientierung des Bienenwolfes II. die Bienejagd. Z. Vergleich. Physiol. 21: 699-716.

Tomanek, G.W. and G.K. Hulett. 1970. Effects of historical droughts on grassland vegetation in the central Great Plains. *In* Dort and Jones 1970, pp. 203-210.

*Tsuneki, K. 1943. On the habit of *Stizus pulcherrimus* Smith. Mushi 15: 37-37.

*Tsuneki, K. 1956. Ethological studies on *Bembix niponica* Smith, with emphasis on the psychobiological analysis of behavior inside the nest II. experimental part. Mem. Fac. Lib. Arts, Fukui Univ., Ser. II., Nat. Sci. 6: 77-172.

*Tsuneki, K. 1963. Comparative studies on the nesting biology of the genus *Sphex* (s. l.) in east Asia. Mem. Fac. Lib. Arts, Fukui Univ., Ser. II., Nat. Sci. 13: 13-78.

---

*References not seen.

Turner, F.B. 1962. Some sampling characteristics of plants and arthropods of the Arizona desert. Ecology 43: 567-571.

Vuilleumier, B.S. 1971. Pleistocene changes in the fauna and flora of South America. Science 173: 771-780.

Wendorf, F. and J.J. Hester (Ed.). 1975. Late Pleistocene environments of the southern High Plains. Publication of the Fort Burgwin Research Center No. 9, 290 pp.

Whitaker, S.H. and E.A. Christiansen. 1972. The Empress Group in southern Saskatchewan. Canadian Journal of Earth Sciences 9: 353-360.

Whitehead, D.R. 1972. Classification, phylogeny and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). Quaestiones Entomologicae 8: 131-348.

Whitehead, D.R. 1976. Classification and Evolution of *Rhinochenus* Lucas (Coleoptera: Curculionidae: Cryptorhynchinae) and Quaternary Middle American zoogeography. Quaestiones Entomologicae 12:118-201.

Willis, H.J. 1967. Bionomics and zoogeography of tigerbeetles of saline habitats in central U.S.A. University of Kansas Science Bulletin 47: 143-313.

Wright, H.E. jr. (Ed.). 1969. Quaternary geology and climate. National Academy of Sciences, Publication 1701.

Wyatt, F.A., J.D. Newton, W.E. Bowser and W. Odynsky. 1937. Soil survey of Rainy Hills sheet. University of Alberta, College of Agriculture, Bulletin No. 28.

APPENDIX

APPENDIX

Philanthus of Alberta

In the intervening years since Strickland (1947) published a list of Hymenoptera of Alberta, new species have been described, additional species have been found in the province and the status of many of the names have changed. It is not known when specimens in the Strickland Collection (University of Alberta) were identified but it is suspected to have been before Strandtmann (1946) published a classification of *Philanthus*. Many specimens in the Strickland Collection were misidentified. In assigning names to the taxa of *Philanthus* found in Alberta I have used the paper by Bohart and Grissell (1975) which treats the California Philanthinae and updates a key to the North American species of *Philanthus*.

Taxa recorded from Alberta but not represented in the Strickland Collection are listed with the references instead of the list of localities following names for which material is available locally. There are 32 species of *Philanthus* known north of Mexico with 15 of these species recorded from or near Alberta. Adults of many of the species of this genus are readily collected on flowers.

The name *Philanthus* is derived from the Greek words *Phila* - love and *Anthos* - flower. The name reflects the flower frequenting habit of the adults.

List of the species and localities of the genus *Philanthus* Fabricius for the province of Alberta.

Philanthus albopilosus Cresson; Empress (11 km south), Orion, Medicine Hat.

P. bilunatus Cresson; Calgary, Claresholm, Cypress Hills, Edmonton, Gull Lake, Medicine Hat, Wabamum.

P. crabroniformis F. Smith; Jenner (8 km east), Lethbridge, Medicine Hat, Tp. 30 Rg. 24 W. 4.

P. gibbosus (Fabricius); Empress (11 km south), Lethbridge, Medicine Hat, Tp. 15 Rg. 22 W. 4, Tp. 27 Rg. 8 W. 4.

P. gloriosus Cresson; Empress (11 km south), Lethbridge, Manyberries, Medicine Hat, Orion, Wardlow.

P. inversus Patton; Buffalo (8 km west). Lethbridge, Manyberries, Medicine Hat.

P. multimaculatus Cameron; Bohart and Grissell (1975, Map 7), Strickland (1947), Medicine Hat.

P. pacificus Cresson; Bohart and Grissell (1975, Map 10).

? *P. politus* Say; west to Saskatchewan, Bohart and Grissell (1975).

P. psyche Dunning; Empress (11 km south), Medicine Hat.

P. pulcher Dalla Torre; Calahoo, Medicine Hat.

P. sanbornii Cresson; west to Alberta, Bohart and Grissell (1975).

P. solivagus Say; Empress (11 km south).

P. ventilabris Fabricius; Empress (11 km south) Lethbridge, Medicine Hat.

P. zebratus basilaris Cresson; Buffalo (8 km west), Lethbridge.

AUTOBIOGRAPHICAL SKETCH

In 1953 I was born in Calgary, where I grew up. An interest in nature developed at an early age, as a preschooler, which focused on bugs. From 1959 to 1971 I was enrolled in public schools; Kensington Road Elementary, Parkdale Junior High and Queen Elizabeth Senior High. A butterfly collection was started in 1965, when I received a butterfly net and butterfly mounting kit as a gift. A few years later I met Hank Oliemans who introduced me to beekeeping. In 1970 I managed my first colony of honey bees. The following year I met John and Bert Carr who stimulated my interest in beetles. They kindly gave me many identified beetles which formed the start of my beetle collection.

In 1971-1972 I attended Mount Royal College as a university transfer student. The summer of 1972 was the start of my bee and wasp collection. In the fall I entered the University of Calgary later graduating in the fall of 1975 with a B.Sc. in Biology. During my stay at the University of Calgary I held a part-time job at Riveredge foundation an Assistant Museum Technician curating the beetle collection. This post was held from 1973 to fall 1975.

From 1973 to 1975 I was treasurer of the Calgary and District Beekeepers Association.

In 1974 I received the Imperial Oil Limited, Higher Education Award, which was renewed in 1975. In 1975 I received the Entomological

Society of Alberta, Prize in Entomology. During the summer of 1975 I went on a collecting trip to the Yukon. In the fall of 1975 I entered the University of Alberta as a Qualifying Graduate Student. In 1976 I was awarded the Entomological Society of Canada Postgraduate Award. From 1976 to date I attended the University of Alberta as a Master of Science candidate.

I have been an avid swimmer through the years and have earned a number of awards, with the highest being the Distinction Award offered by the Royal Life Saving Society of Canada. I also hold Swim Instructor certification, National Lifeguard qualifications and Scuba certification. Other past time activities include hiking, cross country skiing and fishing.